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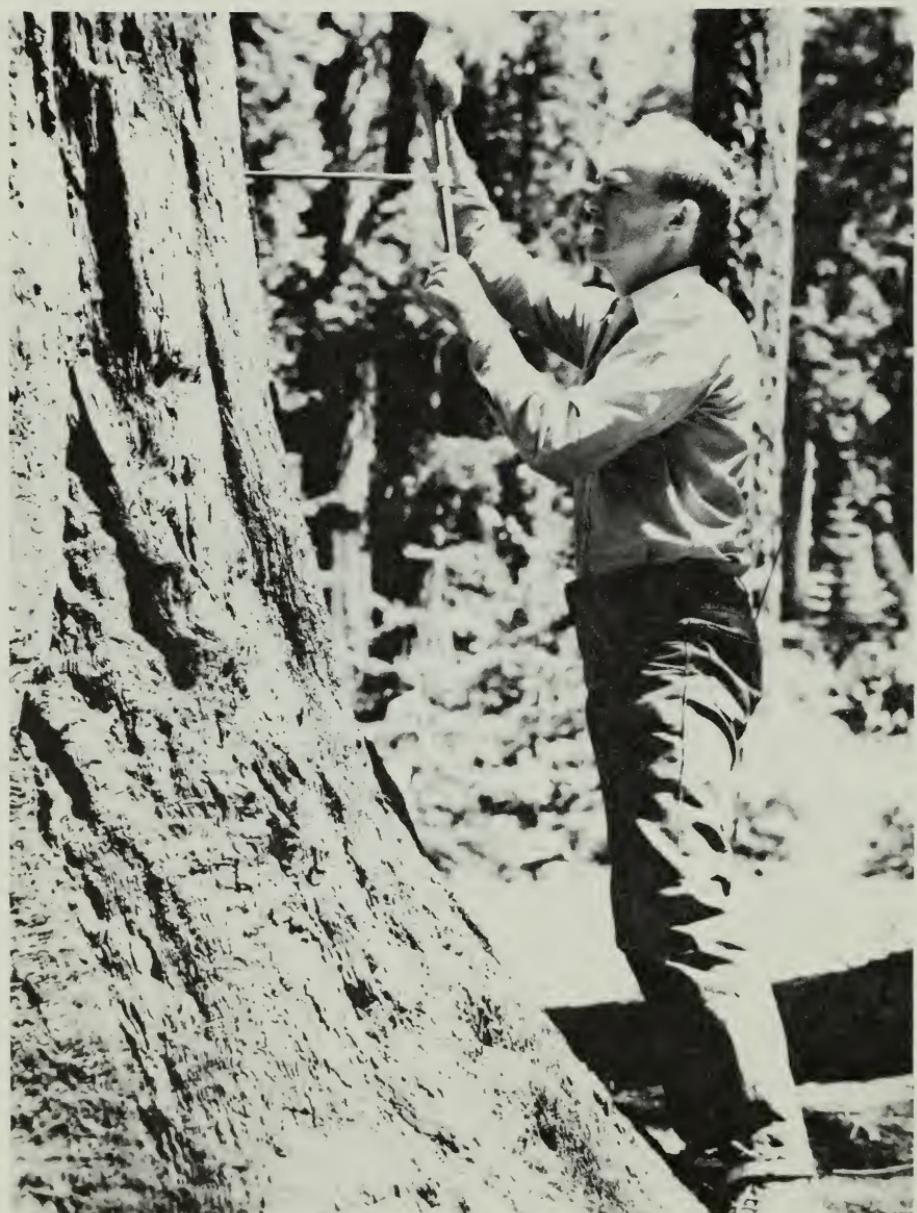
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*Giant  
Sequoia  
Ecology*



Frontispiece. Dick Hertesveldt coring a giant sequoia.

# **GIANT SEQUOIA ECOLOGY**

## **Fire and Reproduction**

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1980

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*To the memory of*  
Richard J. Hertesveldt, Ph.D.

*whose deep interest and concern for the perpetuation of the giant sequoias prompted us to begin these investigations. His encouragement and leadership directed this project and contributed concepts and data upon which this monograph has been developed.*



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# Preface

This monograph is the scientific report of a study which was carried out, in the main, in Sequoia and Kings Canyon National Parks between 1964 and 1975. Our prime concern was to examine the role of fire in the reproduction of the giant sequoia. We present detailed results on some of the ecological relationships of this species and offer them for the better management and interpretation of this majestic tree.

Our interest in this species began between 1956 and 1962 with Dr. Richard J. Hertesveldt's doctoral studies on the effects of human impact on the tree and its environment in the Mariposa Grove of Yosemite National Park. He shifted his impact studies to Sequoia-Kings Canyon National Parks in 1962, where he was initially supported by the Sequoia Natural History Association. During 1963 and 1964 he and his office partner at San Jose State University, Dr. H. Thomas Harvey, discussed the many facets of giant sequoia ecology and together formulated the general outline and goals of the present study. They concentrated on the response of vegetation to fire and, especially, the survival of giant sequoia seedlings. Dr. Howard S. Shellhammer joined Hertesveldt and Harvey in August 1964 to study vertebrates and their impact on the tree. The project received its initial funding, and the first field work was carried out in the summer of 1964. In 1966, when Dr. Ronald E. Stecker joined the research team, the scope of the study was broadened to include the potential interactions of arthropods. Dr. Stecker's earliest work was made possible by the Skelton Foundation and then, like the rest of the group, he was supported by research contracts with the National Park Service. The bulk of the field research was carried out in the summers of 1965 to 1970, plus that of 1974. The untimely death of Dr. Hertesveldt in 1975 shifted the administrative leadership of the study and the coordination of the monograph preparation to Dr. Harvey.

Before he died, Dr. Hertesveldt coordinated the writing of *The Giant Sequoias of the Sierra Nevada* which was submitted to the National Park Service in 1971 and published in 1975. This semi-popular publication combined many of the general results of our study with the giant sequoia lore known to Dr. Hertesveldt. Many technical reports were also generated during the period of the study. These progress and interim reports, the largest of which are those of 1965, 1967 and 1970, are on file in the

Western Regional Office of the National Park Service in San Francisco and at Sequoia and Kings Canyon National Parks. Several (5) technical papers were generated by this study and are cited in the references of this monograph.

This monograph contains a comprehensive synthesis and evaluation of the scientific data from all the phases of this project plus some of Dr. Hartseldt's 1962-64 work on environmental impact. It is the first effort to delineate, identify and evaluate the roles of fire and reproduction in the survival and perpetuation of the giant sequoia. It reports on the first prescribed management burns carried out in a national park in the West. The study was designed to examine many of the ecological relationships involved in the perpetuation of this species. We hope that it will provide park managers with an understanding of the ecology of the giant sequoias sufficient to furnish them with a scientific basis for making realistic resource management decisions. It is also designed to aid the park naturalists in their interpretation of the ecology of the giant sequoia for park visitors.

This study was not designed to study all aspects of the ecology and biology of the giant sequoia. We concentrated on fire and reproduction, while other investigators have studied fungal relationships, carpenter ants, community stability, and the giant sequoia's place in the forest mosaic, to name a few. We have referred to and briefly discussed most of these studies in the text of this monograph and refer the reader to various professional papers for more detailed information. Most of these studies have not been published but are expected to be available soon.

We have organized the monograph into ten separate chapters in a sequence of general introduction and methods, plant relationships, arthropod relationships, vertebrate relationships, and, finally, the summary and management implications. Little was really known about giant sequoia ecology before this study, so we set out to identify the principal organisms and relationships and then concentrated our studies on these. This is best seen in the arthropod and vertebrate chapters where, in each case, a first section of two is devoted to those organisms associated with some stage of the life history of the tree. In the case of the chapter on vertebrates it serves to illustrate how free the giant sequoia is of vertebrate damage and interactions. A second section follows describing the nature and effect of the interaction between insect or mammal and the tree, particularly as it involves seed production and use, or seedling survival. The overall goals of the study are presented in Chapter 2, while Chapters 3 through 9 consider special facets of the study which are then discussed in greater detail. The closing chapter deals with the management and interpretation implications of the study.

Although our studies have clarified certain ecological relationships between the giant sequoia and its environment, many intriguing questions still remain.

## *Acknowledgments*

The studies reported here were made possible by a series of research contracts with the National Park Service. In addition, logistic, supportive and facilitating assistance was given by the National Park Service including the Whitaker's Forest Cooperative Natural Research Station that is operated jointly with the University of California at Berkeley. The preparation of this monograph was also supported<sup>1</sup> by the National Park Service.

We especially acknowledge the personal interest and encouragement of park administrators, biologists, naturalists, rangers, and forestry personnel. Without their involvement this research could not have been accomplished. Of particular value was the help given by John McLaughlin, Peter Schuft, Frank Kowski, and Ray Murphy in setting up the project. Charlie Castro is greatly appreciated for his help in rigging the study trees. David Parsons and Bruce Kilgore provided support and encouragement throughout the many years of this study.

We are most appreciative of the able assistance of Phyllis Stecker. Her curation of insects and ground crewing for the in-tree studies are particularly noteworthy. Richard Benner of Whitaker's Forest was extremely helpful in his numerous kindnesses and maintenance of weather instruments. Daniel Falconer is acknowledged for his assistance on seed germination studies. Also, appreciation is given to Jerry and Wanna Pitts and Margaret Kelley for their assistance.

During the preparation of this monograph we have been severely handicapped by the absence of Richard Hertesveldt. His death in 1975 left us without the leadership that he provided throughout the study. We received assistance, however, from numerous people. Paramount were those who critically reviewed the manuscript. National Park Service scientists David Parsons, Jan vanWagendonk and Orthello Wallis were most helpful. Philip Rundel of the University of California, Irvine; Thomas Bonnicksen of the University of California, Berkeley; Carl Sharsmith of San Jose State University also reviewed the entire manuscript. George Lawrence of Bakersfield College reviewed the two chapters on vertebrates, for which we are grateful.

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# *Abstract*

This study of giant sequoia ecology concentrated on the role of fire as it affected succession and sequoia seedling survival in the mixed-conifer forest of the Sierra Nevada of California. In addition, special consideration was given to the interaction of animals with giant sequoia reproduction, particularly as they affected cones, seeds and young seedlings.

The removal of the litter and duff layers, by fire or manipulation, from the forest floor facilitated the establishment of annual herbs, shrubs and giant sequoia seedlings. Those seedlings growing in soil which had experienced the hottest fires survived at a higher rate than those on other soils. The former seedlings also grew at a faster rate than those on other substrates, reaching a height of over a meter in eight years.

Vertebrate animals were not greatly affected by the fire manipulations and their numbers fluctuated in response to environmental factors other than fire. Most of the vertebrates present in the giant sequoia groves that were studied had little to no effect on sequoia reproduction, with the exception of one species. The Douglas squirrel plays an intimate role in reproduction by feeding on giant sequoia cone scales and thus aiding in seed dispersal. No vertebrates selected fallen sequoia seeds as a preferred food.

Arthropods associated with the giant sequoia were found to number over 150 species. A few fed on the young seedlings and many were associated with the foliage, bark and wood of mature trees. Cone inhabitants were also few in number, with one beetle playing a significant role in the release of seeds from the cones. The beetle, *Phymatodes nitidus*, mined the main axis of cones causing drying of normally serotinous cones, thus causing them to drop their seeds.

The giant sequoia appears to have a fauna which have evolved a partitioning of the cone substrate. The Douglas squirrel uses the relatively young cones for food while the beetle uses the older cones.

The implications for management of the giant sequoia are that prescribed fires should be employed judiciously and that hot localized fires are best for seedling development. The ultimate objective should be to allow natural forces to range free throughout the groves, thus enabling the giant sequoia ecosystem to be perpetuated much as it was in millennia preceding man's intrusion on the scene.

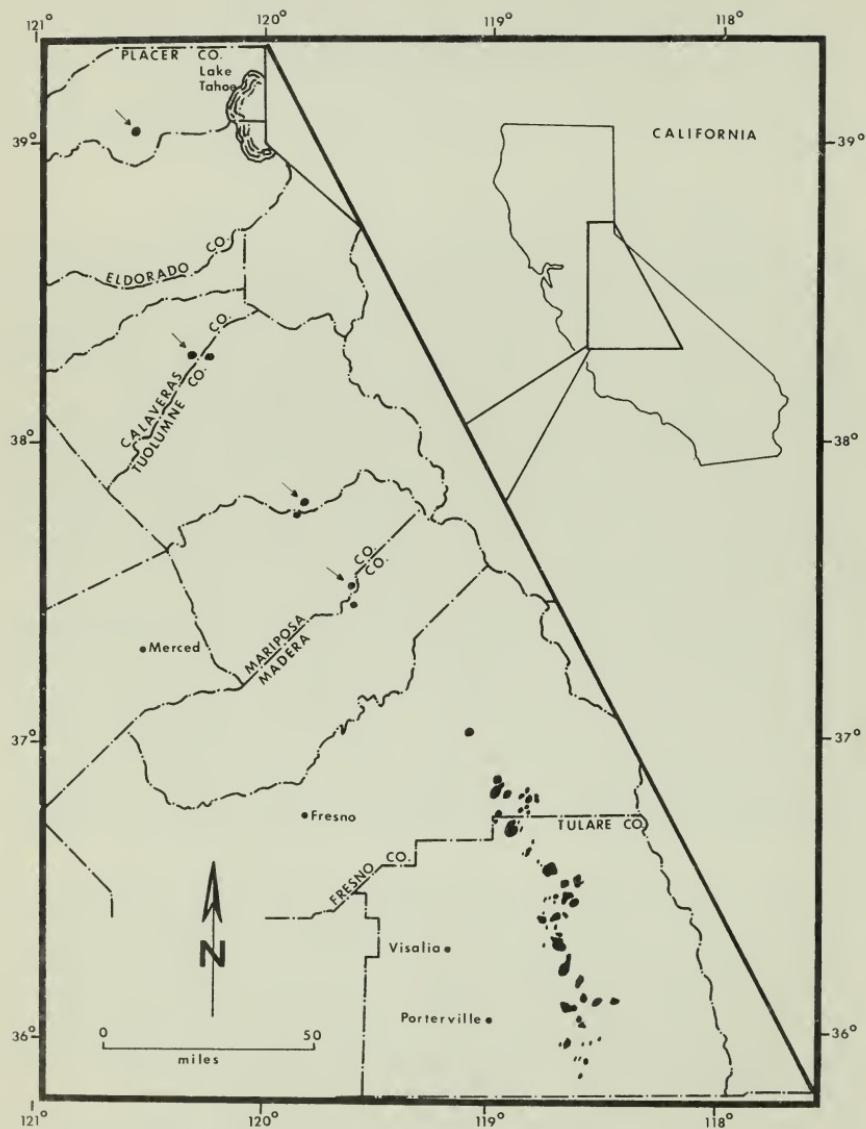


Fig. 1. The range of the giant sequoia (adapted from a map by the California Department of Natural Resources).

# 1

## Introduction

*Howard S. Shellhammer*

Giant sequoias [*Sequoiadendron giganteum* (Lindl.) Buchholz] are among the most magnificent living things on earth. They are gigantic in size, beautiful to behold, awe inspiring, and have had a long evolutionary history. Once discovered by western man, the giant sequoias were quickly threatened by the lumberjack's saw and axe. Protection came only under the auspices of federal, state and local governments. This protection, however, has been so complete as to preclude the very natural forces which are required for the perpetuation of the species. The absence of fire from the sequoia groves, for example, has created a condition where the subtle, yet relentless, process of ecological succession and the violent force of potential crown fires again threaten the species. Enlightened management is called for to insure their continued existence.

Giant sequoias have a disjunct natural distribution. They are restricted to a series of relatively distinct groves which extend some 420 kilometers (260 miles) along the west side of the Sierra Nevada (Fig. 1). Rundel (1972b) listed seventy-five community units or groves, but there is considerable controversy over what constitutes a grove (Hartesveldt et al. 1975). Giant sequoia groves are mainly restricted to elevations between 1525 and 2290 meters (5,000 to 7,500 feet) but may be found growing naturally as low as 1,220 meters (2,700 feet) or as high as 2,713 meters (8,900 feet). Most of the groves are located in the southern third of their geographical range and in or near Sequoia and Kings Canyon National Parks (Fig. 2). While the groves vary from less than 1 to 1,619 hectares (1 to 4,000 acres) in extent, nowhere does the giant sequoia exist as an extensive pure stand. They are associated with those trees which Munz and Keck (1959) have described as comprising the yellow pine forest community: white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), Ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), black oak (*Quercus kelloggii*), and often Douglas fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*) and/or Jeffrey pine (*Pinus jeffreyi*). The particular combination and frequency of these trees in a given grove depends on elevation, latitude, exposure, soil moisture, and the length of time it has been afforded protection from lumbering and fire. Rundel (1969) has pointed out that there is no other species of higher plant found only in association with giant sequoias. Hence, even though giant sequoias are

clearly dominant in the mixed coniferous forests in which they occur, they cannot be considered to constitute a distinct plant community in themselves, for as Dice (1952) has suggested, a plant community should have at least two species in common.

Giant sequoias were more widely spread and probably occurred in continuous forests in the past. The earliest close relatives of the present species, *Sequoia reichenbachi* and *S. couttsiae*, were distributed throughout Greenland, Alaska, Canada, and England during Cretaceous and Tertiary times (Chaney 1951). Fossil sequoias considered to be directly ancestral to the present giant sequoia are found in Miocene deposits in Idaho (Axelrod 1959, 1964). A more recent direct ancestor, *Sequoiadendron chaneyi*, has been described by Axelrod (1962) from a Pleistocene forest in western Nevada. Giant sequoias moved southwestwardly during the late Tertiary as they vanished from the rest of their former range; *S. chaneyi* disappearing from Europe as late as the Pleistocene (Martin 1957). Axelrod (1964) has proposed that the southwesterly migration from Idaho to California was induced by the changes in climate accompanying the gradual rise of the Sierra Nevada. Winter temperatures became more severe in the north, and summer precipitation decreased in the east during the time of migration (Wilson 1928). Hertesveldt et al. (1975) postulated that the giant sequoias crossed the Sierra Nevada in several places and became



Fig. 2. A portion of the Giant Forest Grove in the Crescent Meadow area of Sequoia National Park.

established on the western slope long before the mountains attained their present height.

Numerous hypotheses have been offered to explain the present, narrow, disjunct distribution of giant sequoias. Muir (1876), Stark (1968a, 1968b), Wulff, Lyons and Dudley (1911), and Shinn (1889) all suggested that giant sequoias have a narrow range of tolerance to climatic factors. Most of these authors, especially Muir, envisioned glaciers and cold air drainage as possible factors in disrupting the postulated continuous distributional pattern. Winter cold has often been mentioned, but is poorly understood as a potential factor in limiting growth (Hartesveldt et al. 1975). Soil apparently plays a minor role as a controlling factor, in as much as the parent rock material varies considerably between groves. Giant sequoias have grown vigorously when planted in diverse soils throughout the world (Hartesveldt et al. 1975). Rundel (1969, 1971, 1972a) proposed that the present boundaries of the groves are controlled by an interaction of soil moisture, temperature and the ecological tolerance of the seedling stage. We adhere to this view, as do most students of giant sequoia ecology at the present time.

Giant sequoias were first discovered by western man in 1833 and again in 1852, when their "discovery" was more widely publicized (Hartesveldt et al. 1975). Lumbering began during 1852, and whole groves were being cut down by 1856. The first efforts to preserve some of the groves began soon after their second discovery in 1852. The Mariposa Grove, which is now part of Yosemite National Park, was deeded to the State of California by the federal government in 1864 to be administered as a state park. Additional groves were protected with the establishment of Yosemite, Sequoia and General Grant National Parks in 1890. Other groves were given protection by federal, state and private actions between 1890 and 1940. The last remaining large tract of unprotected sequoia land was added in 1940. In that year the Redwood Mountain Grove, measuring 1,506 hectares (3,720 acres), was incorporated into the newly created Kings Canyon National Park. At present more than 92% of all sequoia grove acreage is under public ownership.

Lumbering continued sporadically until the mid-1950s, by which time approximately 34% of the original total acreage had been cut. Current policies of the various governmental agencies prohibit lumbering of giant sequoias on public lands, and little lumbering of this species is conducted on the remaining private lands. Since fire suppression also has been a general policy of the controlling agencies, most groves have been rigidly protected from fire. Although they have received a full measure of protection, the trees have been the subject of but a few research investigations. The recognition of the need for more sound information regarding these trees and their requirements for survival provided the basis for the current study. Findings of these investigations are reported in this publication.

The management of giant sequoias was one of passive preservation until approximately ten years ago. The change to an active, research-supported management plan, especially on the part of the National Park Service, was stimulated by a series of events. A considerable body of evidence was accumulating on the ecological role of fire in the Sierra Nevada in general and in giant sequoia groves in particular. Scientists were reporting, as well, on the changes taking place in the protected groves, both in the nature of human impact and the increased fire danger from increasingly dense vegetation and fuel accumulation. Finally, the Leopold report of 1963 urged that biotic associations in each national park be maintained, or where necessary *recreated*, as nearly as possible in the condition that prevailed when the areas were first seen by European men.

The role of fire was noted as early as 1878 by John Muir. Mason (1948) noted that sugar pines decreased in number in areas devoid of fires for an extended period of time. Both Biswell (1961) and Hertesveldt (1963, 1964) suggested that fires burned through Sierran communities with a degree of regularity before the advent of western man. Hertesveldt (1963) documented the occurrence of fires in the Mariposa Grove of Yosemite National Park by analyzing cores taken from giant sequoias. He and other scientists postulated that frequent surface fires maintained a more open forest prior to the arrival of European man (Weaver 1947, 1951, 1964; Biswell 1967; Hertesveldt 1963; Hertesveldt and Harvey 1967; and Kilgore 1971, 1972). Show and Kotok (1924) suggested, however, that crown fires did not accompany surface fires as the former were virtually nonexistent in the Sierra Nevada during pristine times, and this hypothesis has been supported by Kilgore and Sando (1975). Kilgore (1973) summarized the present outlook on the role of fire in a mixed-conifer forest. He stated that "fire (1) prepares a seedbed, (2) cycles nutrients within the system, (3) adjusts the successional pattern in various ways, (4) modifies conditions that favor wildlife, (5) influences the mosaic of age classes and vegetation types, (6) alters numbers of trees susceptible to attack by insects and disease, and (7) both reduces and creates fire hazards." He further recognized that each of these functions is affected by fire intensity and frequency. Most of these functions will be discussed in various parts of the present monograph.

The studies of Hertesveldt (1962, 1964) on the effect of human impact on the giant sequoias of the Mariposa Grove of Yosemite National Park provided the basis for a change in attitude toward grove management. He suggested that trampling about giant sequoias may increase, rather than decrease, their rate of growth by reducing other plants which compete for soil nutrients and moisture. He and Beetham (1962) and later Stark (nee Beetham 1968a, 1968b), demonstrated that the absence of sequoia reproduction under protected conditions is due to the fact that young giant sequoias are intolerant of shade. Giant sequoias are favored in earlier

stages of succession which may be created when fire disrupts the climax community. Each author showed that even though germination occurs under shaded conditions, seedling survival is severely curtailed. Both reported that seedlings survive best in bare mineral soil, but that the seedlings have very little chance of becoming established when the seeds germinated on top of a thick layer of litter and duff that accumulates in the absence of periodic fire. Hertesveldt (1964) concluded that the advanced plant succession found in present-day groves is increasing the opportunity for large crown fires which both he and Show and Kotok (1924) determined were absent in pristine times.

Finally, the Leopold report (1963) was important in creating a "climate" for a new approach to park management. Earlier, Olmstead (1952) and Wright (1933) had both urged broad ecological studies be conducted to provide the basis for park management. Hertesveldt (1962, 1964) recognized the need for further research on the giant sequoia. The Leopold Report (1963), which was developed by a special committee appointed by Secretary of the Interior Udall, stressed the ecological complexity of the national parks and implied that a more thorough understanding of each area was necessary in order to effectively manage them. The present study has been carried out with this philosophy in mind. It is an attempt to provide some of the basic information necessary to the scientific management of sequoia groves.

Giant sequoias have long been associated with fire (Hartesveldt 1964). They possess many ecological adaptations to fire. They have a thick bark which helps to insulate them from heat. They shed enormous numbers of seeds which have the greatest chance of success when they fall on soil cleared by fire or erosion. The seedlings are intolerant to shade. They are often overgrown by shade-tolerant plants which crowd in as succession proceeds and which generally increase the chances of the needed surface fires. But fire, it should be noted, is but one part of the ecology of these trees.

Our intent, in the light of the factors previously discussed, has been to study the general ecology of the giant sequoia so that the role of fire and other factors may be more completely understood, and to provide information necessary for the development and implementation of an ecologically sound resource management plan.

Holloway (1954) said it best when he suggested that studies of fire ecology must be "founded in a deep appreciation of the forest, of its complex interrelationships of all its component parts. And, since the forest is an ever-changing, living community, understanding also demands unrelenting study of all trends in forest evolution, man-made or natural. For a single forest, the complex actions and interactions of all plants, soil, animals, microorganisms, and man together with all factors of climate, topography, lithology, and history must be studied together and in synthesis."

# Objectives, Design, Study Areas, and Methods

*Howard S. Shellhammer*

## *Objectives of the study*

Fire has long been a part of the ecology of giant sequoia groves. We hypothesized that it could be used as a tool to manage present-day groves, but we recognized that much more of the ecology of the species involved must be known to do so effectively. Therefore we felt we needed to:

1. determine specifically the role of fire and other disturbance factors in seed distribution and germination, and in seedling establishment and survival;
2. understand more adequately the position of the giant sequoia in the ecological successional pattern;
3. determine the role of arthropods, birds and mammals in the life history of the giant sequoia;
4. provide the National Park Service and other agencies that manage giant sequoias with data upon which to establish ecologically sound management and interpretive action programs.

## *Design*

The general design of our studies was as follows:

1. Four study areas were established. These were chosen so as to differ in patterns of fuel accumulation, substrate, plant composition of the ground cover, and, to some degree, exposure and soil moisture. All areas were similar in that they generally lacked recent sequoia regeneration and were near fire roads and water sources.
2. Half of each study area was divided into manipulated and control portions. Each portion was studied before, to some extent, during and in the first, third and ninth years after manipulation.
3. One to three different management techniques were used in the manipulated areas, depending upon their topography and pattern of fuel accumulation.
4. The major thrusts of our studies were the changes in vegetation associated with manipulation, survival of giant sequoia seedlings and the interactions of invertebrates, birds and mammals with the

various stages in the life cycle of the giant sequoia. Each seedling produced in the manipulated portions of the study areas was to be individually identified and followed throughout the period of the study, allowing us to correlate substrate conditions and seedling survival.

### The study areas

The four study areas were located in the Redwood Mountain Grove in Kings Canyon National Park (Fig. 3) at elevations between 1646 and 2042 meters (5400 and 6699 ft). Each area was in an advanced state of plant succession and contained little or no recent reproduction by giant sequoias. Most areas had about 15 giant sequoias per hectare (6 per acre) and most of the trees exceeded 3 meters (10 feet) in diameter at breast height (dbh). Although fire had been excluded from the Redwood Mountain Grove for 70 to 80 years, the grove was disturbed by a small shingle operation that was carried out until 1940 when the grove became part of the park.

An abundant understory of white fir (*Abies concolor*) and some incense cedar (*Calocedrus decurrens*) existed in most parts of the grove. Large canopy trees, in addition to the giant sequoia, included white fir, sugar pine (*Pinus lambertiana*) and Ponderosa pine (*P. ponderosa*). A thick layer of litter existed over most of the grove, with sweet cicely (*Osmorhiza chilensis*), white hawkweed (*Hieracium albiflorum*), and trail plant (*Adenocaulon bicolor*) as dominant species of ground cover.

A small stream, Redwood Creek, ran beside or near three of the four areas and provided a normal mid-Sierran riparian association of willow (*Salix* spp.), western azaleas (*Rhododendron occidentale*), creek dogwood (*Cornus californica*), mountain alder (*Alnus tenuifolia*), and California hazelnut (*Corylus rostrata*). The soil material in the study areas was derived primarily from metamorphic schists, although granitic parent material was present in other parts of the grove. The soil was generally of a gray-brown podzolic type, and its texture varied from fine sand to sandy loam.

The annual precipitation in the grove ranged from 46 to about 230 cm (18 to about 90 inches) depending upon altitude, exposure or the year. Summer storms were light and infrequent. Most of the precipitation occurred in the form of snow between October and April. The average depth of the snow in the grove was 1.5 to 1.8 meters (5 to 6 ft). Temperatures varied during the period of the study from average highs and lows of 4.4°C and -1.1°C (40°F and 30°F) in the coldest months to 26°C and 10°C (80°F and 50°F) in the warmest months. The coldest temperature recorded in a field area during the study was -11.6°C (11°F).

Access to each of the areas was by a fire road which descends from Redwood Saddle and parallels Redwood Creek (Fig. 4). Although this road is used as a trail, it is closed to public vehicular traffic, thus the public access to the areas was slight.

Two study areas, Ridge and North (Fig. 4), measured 1.8 hectares (4 acres) each and the other two, Trail and South, were each 3.6 hectares (8 acres) in size. Ridge Area was located on the upper portion of the east-facing slope of Redwood Mountain near Redwood Saddle. It was the steepest (34% slope) and the driest area. North Area was situated on a

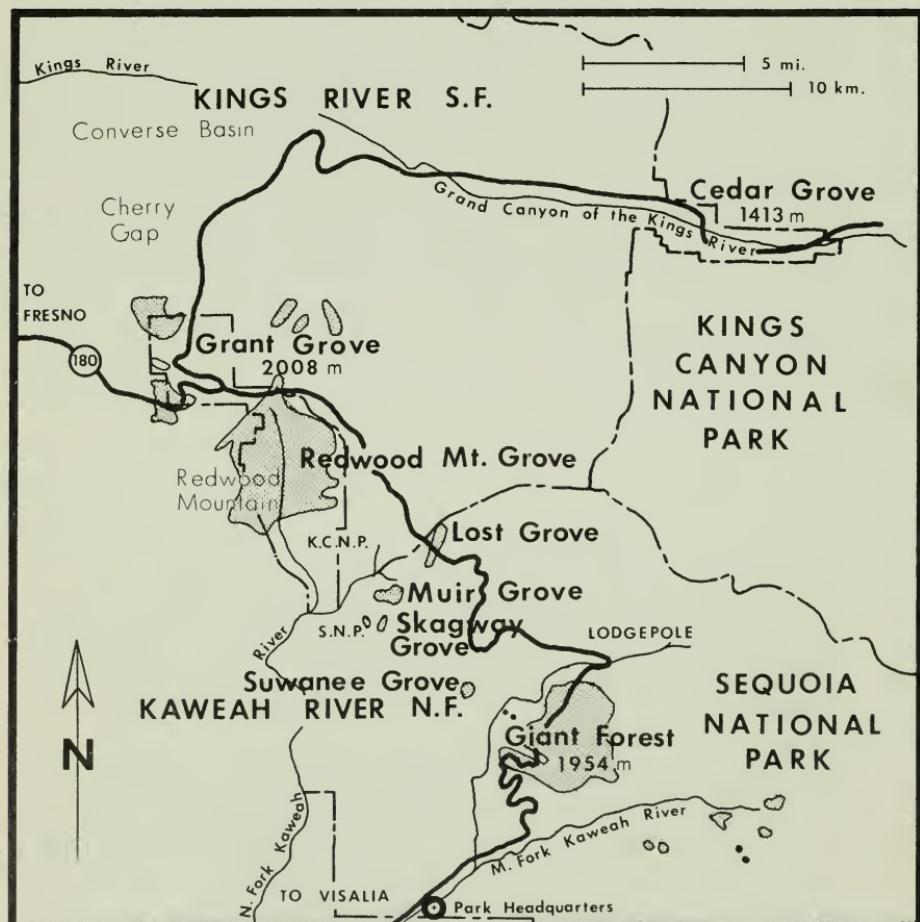


Fig. 3. Location of Redwood Mountain Grove, the site of these studies.

small, flat, old flood plain on the west side of Redwood Creek and was relatively mesic. It had the greatest initial understory of young white fir and incense cedar of any of the areas.

The area with the second steepest slope (17%) was Trail Area. It contained the greatest amount of fallen trees and litter.

South Area, located on a southwesterly facing slope across Redwood Creek from Trail Area, was the most mesic site, with a seep occurring near the middle of the manipulated area. For a tabular comparison of the four areas see Table 1.

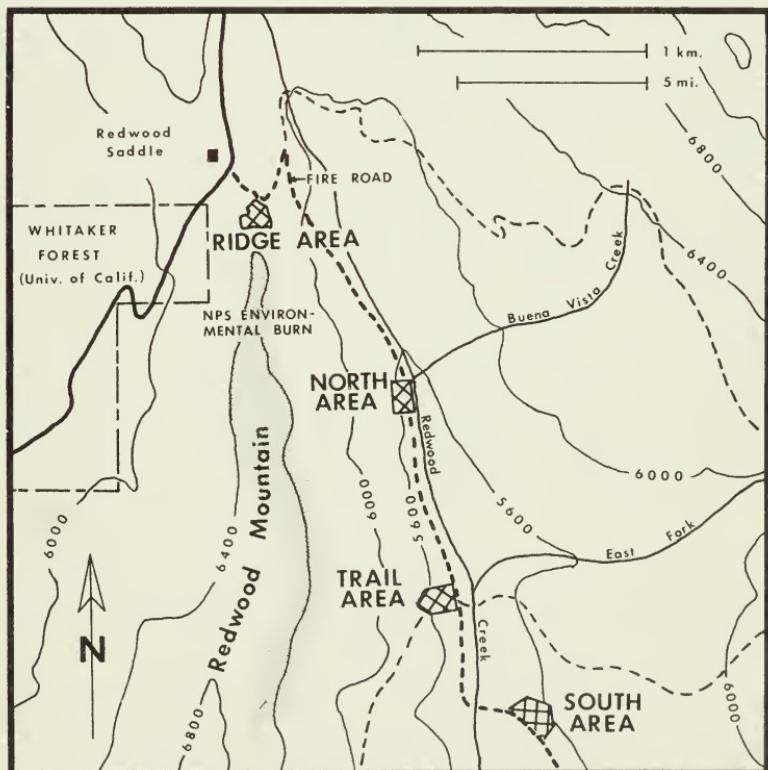


Fig. 4. Study areas in the Redwood Mountain Grove, Kings Canyon National Park.

**Table 1.** Comparison of the four study areas

	Ridge	North	Trail	South
Elevation	1,905 m (6,250 ft)	1,707 m (5,600 ft)	1,611 m (5,450 ft)	1,611 m (5,450 ft)
Area, manipulated and control	1.8 ha	1.8 ha	3.6 ha	3.6 ha
Number of mature giant sequoias	14/ha	15/ha	9/ha	8/ha
Relative amount of downed material	light	moderate to heavy	heavy	moderate
Relative amount of ground cover	sparse	moderate	sparse	moderate
Date of manipulation	1965	1964, 1965	1965	1966
Type of manipulation	surface burning	logs piled by bulldozer, burn piles, little surface burning, piles reburnt in 1965	logs piled by rubber- tired loader, burn piles, some surface burning	wood and brush into windrows by bulldozer, windrow burns, moderate surface burning

## Methods

The vegetation of Ridge, North and Trail Areas was sampled by means of regularized rectangular plots. Woody vegetation taller than one meter was sampled by  $5 \times 20$  meter plots, while all other vegetation was sampled by  $1 \times 2$  meter plots. The initial inventories were carried out in these three areas in the summers of 1964 and 1965. South Area was sampled by the line intercept method for small vegetation and the random pairs method for tree species in 1966 (see Chapter 4).

Surface burning of the litter and ground vegetation was possible only in Ridge Area. North, Trail and South Areas contained so many dead snags and downed trees as to preclude a similar use of fire throughout most of each of those areas. After felling the snags, the debris in each of these areas was piled or windrowed and then burned. These experimental fires were the first such fires in National Park forests in the West.

A cleat-tread bulldozer was employed in North Area to move and pile logs. To minimize the physical disturbance to the soil, a rubber-tired Hough Payloader was employed for the same purpose in Trail Area. A bulldozer with a brush blade was used to move logs into windrows for burning in South Area. Surface burning was carried out wherever possible after mechanical manipulation in each of the areas. During these treatments the land surface of each area was both burned and physically disturbed, and the crown canopy was partially opened.

Vegetational changes were assessed during the year after burning (1965 or 1966, depending on the area), then in 1969 and again in 1974 (Chapter 4). Seedling giant sequoias were individually identified and monitored semiannually for nine years (Chapter 5). Cone loads of giant sequoias, i.e. the numbers of cones per tree, in the areas were assessed (Chapter 5 and 9), as were the number of seeds per cone and the rate of seed fall (Chapter 5). Measurements of physical and edaphic factors affecting seed germination and seedling survival were carried out throughout the study (Chapter 3). Increment borings of giant sequoias were made to ascertain growth responses to the manipulations.

Arthropods associated with giant sequoias were identified and studied both from the ground and in two large giant sequoias in Redwood Canyon (Chapter 6). In the later phases of the project arthropods identified as being involved with some stage of giant sequoia reproduction were studied more intensively both on the ground and in the trees (Chapter 7).

Birds and mammals in the areas were censused by direct observation and by mark and release methods of live trapping before and after manipulations (Chapter 8). Seed spot tests carried out on the forest floor were used to assess the preferences of birds and mammals for conifer seeds (Chapter 8). The Douglas squirrel (*Tamiasciurus douglasii*) was identified in the early phases of the study as the one vertebrate that directly

affects reproduction of the giant sequoia. It received intensive study during the latter years of the project (Chapter 9).

Numerous other studies on various aspects of giant sequoia ecology were carried out between 1964 and 1974. They are reported in various parts of Chapters 3 through 9.

Implications of this study for the management and interpretation of giant sequoias are discussed in Chapter 10.

# 3

# Environmental Factors

*H. Thomas Harvey*

## *Introduction*

Several physical factors were measured in the study plots and in adjacent areas during the study period. Soil texture and moisture regimes were assessed during the summer. Soil temperatures during experimental burning were also explored, as were normal soil temperatures. Typical weather measurements included temperature and relative humidity, while precipitation data were obtained from nearby sites.

The amount of sunlight striking the forest floor was determined at specific sites and related to plant species present. Also litter and duff accumulations were assessed and related to plant species.

## *Methods and materials*

Soils of the study sites were assessed as to composition and soil moisture. Soil composition was determined by taking samples systematically from a depth of from 2.5 to 10.2 cm (1 to 4 in). This depth was selected because it represents the rooting zone of giant sequoia seedlings. In addition to the 12 samples taken from the study areas, 115 samples were taken from 12 different giant sequoia groves. The samples were taken as opportunity permitted. The samples were analyzed by Curtis and Tompkins, Ltd. of San Francisco for total nitrogen, potassium ( $K_2O$ ), phosphorous pentoxide ( $P_2O_5$ ), and pH.

Soil moisture determinations were made by using gypsum soil moisture blocks (Bouyoucos and Mick 1940). The blocks were first soaked in water and then placed systematically at various sites within the treated and control sections. Blocks were placed at depths of 7.6, 15.2 and 30.5 cm (3, 6 and 12 in). They were monitored by the use of a Delmhors<sup>t</sup> ohmmeter with readings converted to percent total weight after standardization for the type of soil, namely loamy sand. Gypsum soil moisture blocks were also carefully placed in a regularized grid in two of the thick stands of giant sequoia seedlings which came up after treatment, at 7.6 cm (3 in) below the surface of the mineral soil, and monitored throughout the summers.

Soil temperature was also monitored, both as a seasonal variant in control soils and as a characteristic of soils exposed to fire. Soil temper-

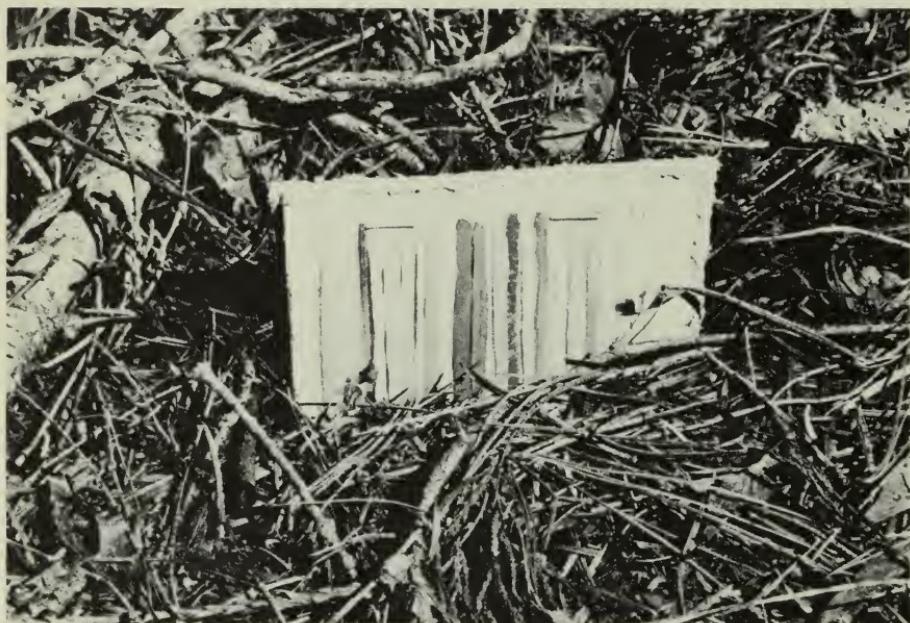


Fig. 5. Tempilaq° temperature recording device in place.

Fig. 6. Litter and seedfall panels with adjacent exclusion section.



atures were measured at the 30.5 cm (1 ft) level by a recording soil probe max.-min. thermometer placed systematically in North Area. Soil temperatures at or near the surface were measured by a thermistor with constant recording on a Rustrac tape recorder. These measurements were made at sites selected for their extreme characteristics of open charred soil or deeply shaded conditions.

The soil temperatures during a fire were determined by using Tempilaq° (Fenner 1960). Nineteen fusion temperature paints of Tempilaq° with melting points from 65.6°C (150°F) to 644.6°C (1200°F) at 27.7°C intervals were used. Each temperature sensitive paint was applied to strips of mica 4 or 6 inches in length which were then stapled to a supportive sheet of asbestos. These test strips were carefully placed in the soil with the mica side against the undisturbed soil face. Soil was filled in behind the asbestos sheet and the surface of the mineral soil was marked on the sheet (Fig. 5).

Tempilaq° test sheets were placed at 12 regularized sites in the surface burn in Ridge Area and in two burn piles in North Area. After the prescribed burns both temperature and depth to which it occurred were read off the fused Tempilaq° on the mica sheets.

Weather measurements were made using standard weather equipment. A recording hygrothermograph was placed in a standard weather shed and standardized periodically using a sling psychrometer. Three-pen remote recording thermographs were used, one at each of two locations, to obtain temperature profiles at the soil surface and at depths of 15 cm (6 in) and 1.8 m (6 ft). Temperatures were also periodically taken throughout the height of a giant sequoia. Maximum-minimum thermometers were placed in all study areas and in six other giant sequoia groves. Temperatures in the northernmost grove, the Placer County Grove, and the southernmost grove, the Deer Creek Grove, as well as the highest elevation tree and the lowest elevation tree were also monitored. Temperatures at near ground level were measured using a field portable thermistor which recorded on a Rustrac two-pen recorder powered by a 12 volt wet battery.

Precipitation data were extrapolated from records kept throughout the year at nearby weather stations.

Light was measured as sunlight striking the forest floor. A chemical light meter in the form of anthracene in benzene was utilized with the change in optical density being read with a Bausch and Lomb Spectrophotometer 20. The method is essentially that suggested by Dore (1958) and modified by Waring and Major (1966). Two vials containing the liquid mixture were placed at each site over a 24 hour period. To assess the relationship of various ground cover plants to light, the pairs of vials were placed on grey felt in the centers of each regularized ground cover plot.

After exposure the vials were collected and the optical density of the fluid was determined.

The accumulation of litter and duff under a forest canopy are of considerable ecological significance. To measure rate of fall, 1 meter square catch panels were placed at 25 sites on the regularized grid of North Area and measured after 9 months of litter fall (Fig. 6). Litter and duff depths *in situ* were measured at 50 of the 1 × 2 m plots. A clean cut was made at the four corners and in the middle of each plot. The depth of litter and duff was then measured in each profile, and an average of the five measurements was used as the depth of litter and duff for each plot. Six classes of duff and litter depth were determined in 2 cm increments running from 0 to 12 cm (0 to 30 in).

## Results

The surface soils of the study areas were essentially sandy loam with only two samples in the sandy loam category. The silt and clay fractions averaged 13% and 18% respectively, which is in the sandy loam soil type designation, using the U.S.D.A. Soil Textural Class triangular diagram (USDA 1957). The majority (60%) of those samples of soil were in the loamy sand category, 10% were sandy loam and 30% were sand.

The average pH value was 7.2 for the study area soils, whereas in the study of other sequoia groves the average pH was 6.9. The range of pH for the study area soils was from 6.9 to 7.3, while those of the other groves were from 6.0 to 7.5. Therefore it appears that the acidity of soils in which giant sequoias grow is near neutrality. The major nutrients at the study areas were within the range of those found in other sequoia groves.

Total nitrogen averaged 0.28% in the samples from the study area, while it was 0.20% in the 115 samples taken from other sequoia groves. The total nitrogen showed a significant drop in the highly heated soils. From two samples under burn piles only 0.01% and 0.02% total nitrogen were measured, whereas the average for 10 samples outside burn piles was 0.28%. The phosphorous level was 11.5 ppm for the study area samples and 15.5 ppm for the 12 grove survey. The phosphorous level of the study site samples averaged 0.7 ppm while the larger study samples mean was 0.87 ppm.

Soil moisture varied from year to year. For example, the soil moisture at a depth of 7.6 cm (3 in) in a dense stand of giant sequoia seedlings in Trail Area, was significantly higher for a longer period in 1969 than in 1966 (Fig. 7). Similarly, when soil moistures at varying depths from 30.5 cm (1 ft) to 7.6 cm (3 in) were compared in North Area during the summers of 1966 and 1969 the depletion was greatest in 1966 in rate and amount of decrease.

The highest soil surface temperature recorded was 70°C (158°F) on

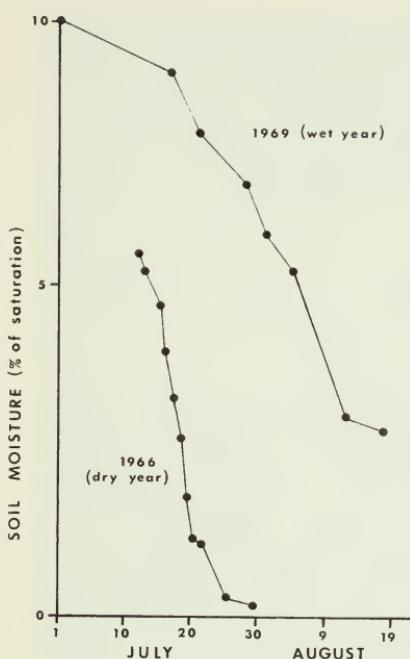


Fig. 7. Soil moisture at 7.6 cm (3 in) among giant sequoia seedlings.

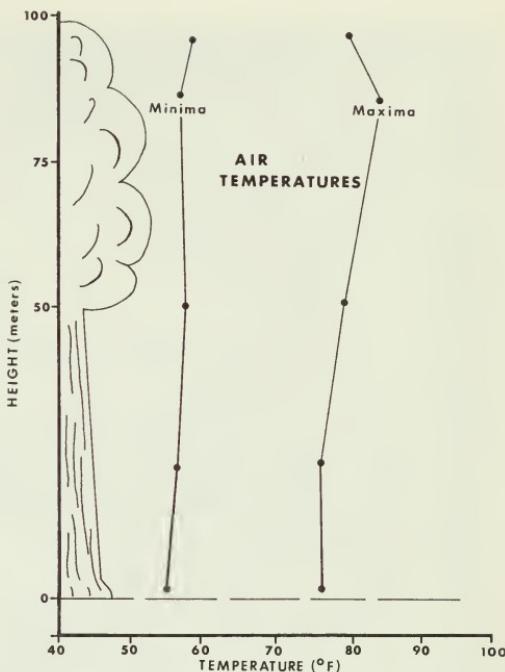


Fig. 8. Summer mean maxima and minima in giant sequoia canopy.

sunlit ground char. Over a three year period the recording 30.5 cm (1 ft) probe thermometer recorded a maximum of 16.6°C (62°F) and a minimum of 10°C (50°F) at the one foot depth. A summer profile of temperature from near the ground to 85.3 m (280 ft), near the top of a giant sequoia, is shown in Fig. 8.

Soil temperatures during fires varied considerably from site to site depending on the amount of fuel present (Fig. 9). Temperatures under burn piles ranged as high as 399°C (750°F) 2.5 cm below the surface (Hartesveldt and Harvey 1967). Some surface burns resulted in Tempilaq® readings up to 260°C (500°F) at mineral soil surface and to as deep as 5 cm (2 in). In some spots soil surface temperatures exceeded 649°C (1200°F), while in others the fire was not hot enough to consume the fuel (Fig. 10).

In order to characterize the mesoclimatic conditions at the study areas, comparisons were made with longer periods of weather records at Grant Grove and Whitaker's Forest. Grant Grove is at an elevation of 1980 m (6500 ft) and 4.8 km (3 miles) from the study sites. Whitaker's Forest is at 1645 m (5400 ft) and about 1.6 km (1 mile) from the study sites. The study areas range from 1646 m (5400 ft) to 1890 m (6200 ft) in elevation and thus are very similar to the above reference locations.

In Fig. 11 and Fig. 12 the three locations are compared as to their mean



Fig. 9. Light ground fuel in foreground, heavy fuel in background.

maximum and minimum temperatures throughout several years. By inspection of the charts it is evident that Grant Grove and Redwood Canyon (study site) were most alike, while Whitaker's Forest was warmer on the average. This was probably due to its lower elevation and the fact that it is on a west facing slope, not in a canyon. The lowest temperature recorded for the Redwood Canyon sites was  $-11.6^{\circ}\text{C}$  ( $11^{\circ}\text{F}$ ).

During July and August of 1966 temperatures were recorded at three levels: 2.54 cm (1 in) below the soil surface, 15 cm above, and 1.8 m above, among dense stands of giant sequoia seedlings in Trail and Ridge Areas (Table 2). The soil at 2.54 cm below the surface reached the highest temperatures, except for the maximum temperature at Ridge Area. The 15 cm temperatures at Trail Area were as low or lower than those at the other two elevations. Ridge Area is located almost 244 m (800 ft) higher in elevation than Trail Area and is not subject to the same cold air drainage. The maxima at the 1.8 m level on Ridge Area were lower than those at Trail Area, while the minima were higher.



Fig. 10. Patchy fuel consumption by surface fire.

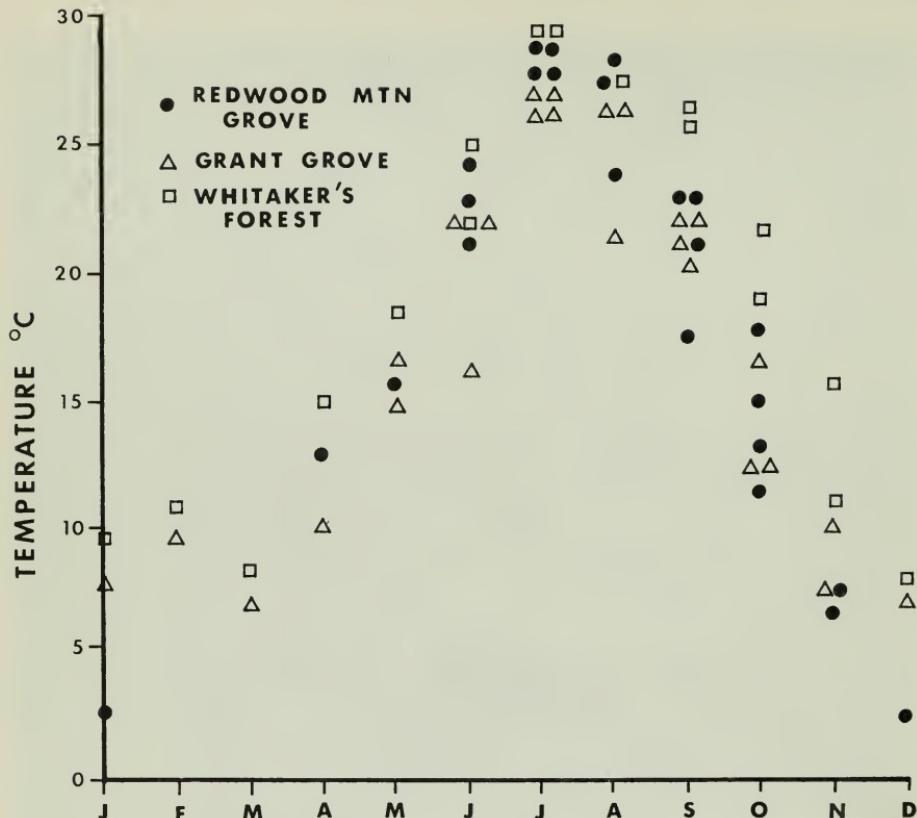


Fig. 11. Mean maxima for Redwood Mountain Grove, Grant Grove, and Whitaker's Forest.

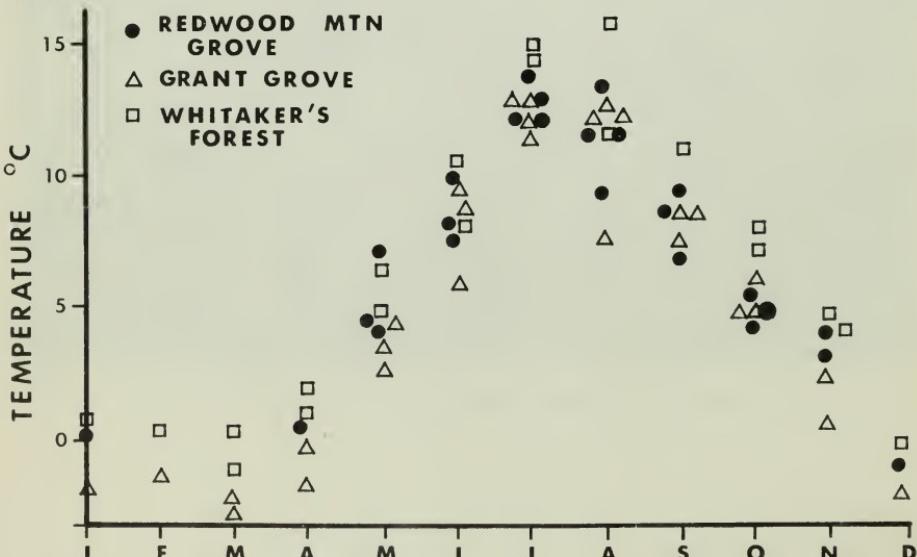


Fig. 12. Mean minima for Redwood Mountain Grove, Grant Grove, and Whitaker's Forest.

**Table 2.** Microclimate temperature (°C) gradients at Trail and Ridge Areas during July and August 1966.

Probe elevation above soil surface	Trail				Ridge			
	Max	Min	Mean Max	Mean Min	Max	Min	Mean Max	Mean Min
1.8 m (6 ft)	37.5	4.0	32.4	9.7	35.5	5.5	28.4	16.7
15 cm (6 in)	37.5	4.0	30.6	9.1	36.5	6.0	30.8	15.1
-2.5 cm (1 in)	38.0	8.0	34.4	12.9	28.5	10.5	23.5	16.7

Precipitation at the study sites is probably very close to that of the reference locations due to the similar elevations and close proximity. A comparison of precipitation data from Whitaker's Forest and Grant Grove revealed a high correlation ( $r = .94$ ). In twelve months for which there were data, and in which over 2.54 cm (1 in) fell per month, a total of 209.1 cm (82.33 in) fell at Grant Grove while 209.5 cm (82.50 in) fell at Whitaker's Forest. This was over a four year period during which the greatest difference between months was less than 7 cm (2.75 in), and all but two of the months showed a difference of less than 3 cm (1.2 in). It was assumed to be adequate to use the precipitation data from either of these areas to elucidate the response of plants to precipitation at the study sites.

Fig. 13 presents the precipitation patterns at Grant Grove for the four years at the beginning of our study. It is of interest to note that there were alternate wet and dry years and that in the wet years considerable precipitation occurred during the later winter and spring, whereas in the dry years most of the precipitation fell in the early winter. The total seasonal precipitation for each period was: 1965-66, 78.1 cm (30.75 in); 1966-67, 172.7 cm (68 in); 1967-68, 56.8 cm (22.4 in), and 1968-69, 222.1 cm (87.45 in). The mean annual precipitation for Grant Grove during the study period of 11 years was 113 cm (45 in). The mean seasonal precipitation was 109 cm (43 in) and the unusual heavy precipitation during the 1968-69 season was over twice normal.

Although long range data are not available for the study site, it is located near Grant Grove, for which there is a long range record. Fig. 14 presents the climograph for Grant Grove. As with much of California, the climograph indicates warm, dry summers and relatively cold, wet winters and it is assumed that the study site would have a climograph very similar to Grant Grove.

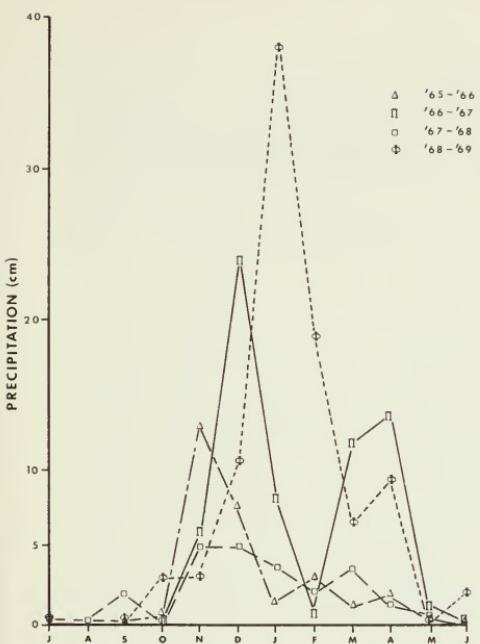
Relative humidity measurements showed typical high morning readings and relatively low afternoon readings. The monthly means for maxima

and minima were typical for a mesic forest habitat (Fig. 15). The lowest values were in late summer and early fall, with August having the lowest mean values. Of special interest was the extreme low relative humidity recorded for August during four consecutive years (1967-70). The mean for July was 27% and for September it was 26%. The range of values did not overlap for August and the other two months. The lowest relative humidity recorded was 16% in August of 1970. These data are particularly important in evaluation of giant sequoia seedling survival as discussed in Chapter 5.

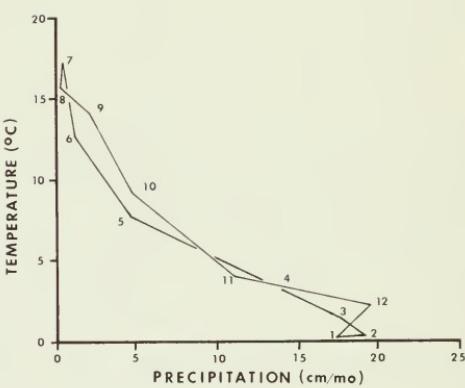
Sunlight striking the sample plots in the study areas varied from 0 to 41% of full sunlight. The average percentages for the various areas are of dubious value because of the relatively few points sampled, i.e. less than 50 per hectare. However, they do help quantify the general impression that North Area is more open than Ridge or Trail (Table 3).

**Table 3.** Mean percentages of sunlight striking the forest floor at sample plots.

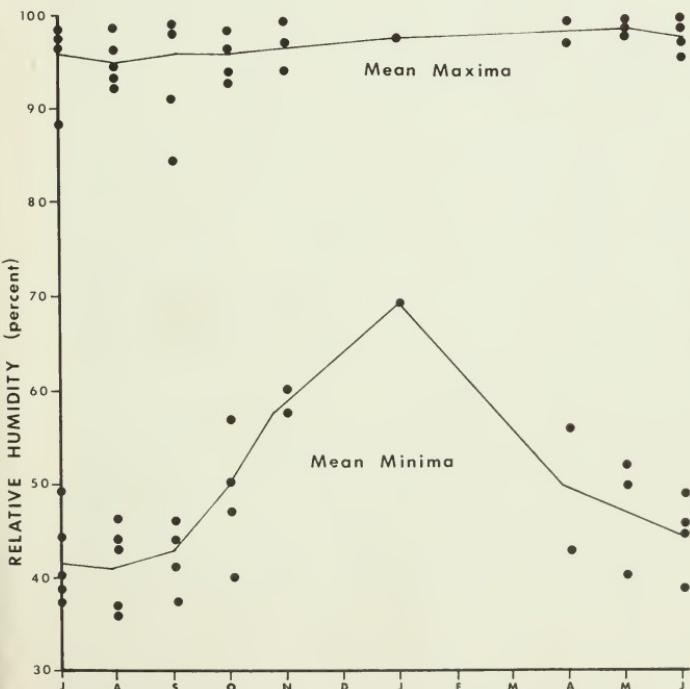
Area	Section	Percentage of full sunlight	
		1965	1966
Ridge	Manipulated	8.5	8.1
	Control	9.1	8.5
North	Manipulated	23.5	18.8
	Control	13.7	11.2
Trail	Manipulated	4.6	10.4
	Control	4.8	6.3



**Fig. 13.** Precipitation at Grant Grove  
(data from National Park Service)  
(4.8 km (3 mi) from study sites).



**Fig. 14.** Climograph of Grant Grove.  
(4.8 km (3 mi) from study sites).



**Fig. 15.** Monthly average  
maxima and minima  
relative humidities,  
North Area, 1966-69.

## *Discussion and summary*

The range of physical attributes within which the giant sequoia ecosystem occurs appears to be moderate. The climate is one in which precipitation varies from 46 cm (18 in) to 152 cm (60 in) with a mean of 112 cm (44 in) per year (Schubert 1962). The minimum temperature recorded during the study period was  $-11.6^{\circ}\text{C}$  ( $11^{\circ}\text{F}$ ), however, Schubert (1962) reports  $-24^{\circ}\text{C}$  ( $-12^{\circ}\text{F}$ ) as the occasional low for giant sequoia communities. Maxima rarely exceed  $38^{\circ}\text{C}$  ( $100^{\circ}\text{F}$ ).

The substrate in which giant sequoias and their associated plants grow was determined to be a loamy sand in 60% of the cases, the remaining were sand or sandy loam. In addition to our studies, Zinke and Crocker (1962) found sandy loam soils in the Merced Grove, the Nelder Grove and Giant Forest. As with many other factors, there is both an advantage and disadvantage to plant growth in these extreme types of soil. The more sand in the soil the less tightly water is held and the less work the plant must do to gain soil moisture (Lutz and Chandler 1946). The disadvantage of these sandy soils is that of rapid percolation beyond the root zone of seedlings. The soil moisture curves for the study areas confirm this tendency, since the 1966 soil moisture levels fell almost to zero by the end of July in Trail Area.

The pH level, both in the study areas and in 12 other giant sequoia groves, was essentially neutral. General absorption of nutrients is maximized by soil pH values near 7 (Daubenmire 1974). Therefore, even if such soils may be relatively poor in nutrients the pH levels are optimal for absorption. The mean total nitrogen level in the study sites was 0.3 %, which is within the range of 0.24–0.45% determined by Zinke and Crocker (1962) as occurring in other giant sequoia groves. Although nitrogen may be reduced immediately after a fire, it is probable that the available nitrogen is actually increased in time (Agee 1973; Viro 1974; St. John and Rundel 1976). Although fire may aid plant reproduction by removing duff and litter so that seeds can reach mineral soil the black char on the surface may increase soil surface temperature to a high degree. This increased heating can lead to desiccation and death of seeds and seedlings in such sites. During fires the penetration into the soil of high temperatures was highly variable. Under burn piles, temperatures of about  $400^{\circ}\text{C}$  ( $750^{\circ}\text{F}$ ) were recorded at 2.5 cm below the surface. Agee (1973) reported a temperature of  $206^{\circ}\text{C}$  ( $403^{\circ}\text{F}$ ) in a white fir–giant sequoia prescribed burn in which litter and duff were the fuel. High temperatures such as these consume surface seeds and small plants, and in the case of the hottest fires, lethal temperatures can penetrate as much as 20 cm (8 in) below the surface. This essentially sterilizes the soil as far as seed germination of many plants is concerned.

# Vegetational Changes

*H. Thomas Harvey*

## *Introduction*

Secondary succession may occur in forest ecosystems after a disturbance such as fire. This succession may be assessed by measuring changes in species composition and their abundance (Horn 1974). The succession we were primarily concerned with followed experimental treatments consisting of mechanical and manual disturbances and fires. The fires were either surface fires or burn pile fires.

The vegetational changes that were monitored consisted of ground vegetation (higher plants up to a meter tall) and trees (single-stemmed woody plants more than a meter tall).

Bonnicksen (1975) has studied the mixed conifer-giant sequoia forest ecosystem in Redwood Canyon immediately northeast of our study areas. He concludes that the primeval forest "consisted of a mosaic pattern of gaps, and approximately even-aged groups of trees and shrubs in various stages of development." He also presented a successional pathways model in which the sequences progress toward a multilayered vegetation unit of pure white fir. However, Bonnicksen suggests that fire, insects, disease, and windthrow probably prevented most of the forest's progressions from reaching the white fir climax stage. Thus the sequoia-mixed conifer forest is more a property of the mosaic than of any single vegetation unit. He concludes that this forest ecosystem consists of "steady state space-time mosaics composed of distinct structurally defined, and successional related, vegetation units." In other words, small areas of different species at different stages of development form a mosaic.

Concern has been expressed by several investigators (Biswell 1961; Hartesveldt 1964; Rundel 1971) that the absences of fire may eventually lead to the succession of white fir in giant sequoia communities, and thus place the relict species, giant sequoia, in jeopardy (Fig. 16.).

One basic objective of these studies was to determine if certain early stage species of low occurrence in the present community would increase in number upon introduction of fire and manipulation, while other more common species might decrease after treatment. It was also an objective of the study to document the rate at which the return to pre-burn conditions was accomplished. The population fluctuations of all the species were



Fig. 16. White fir saplings growing beneath giant sequoias.

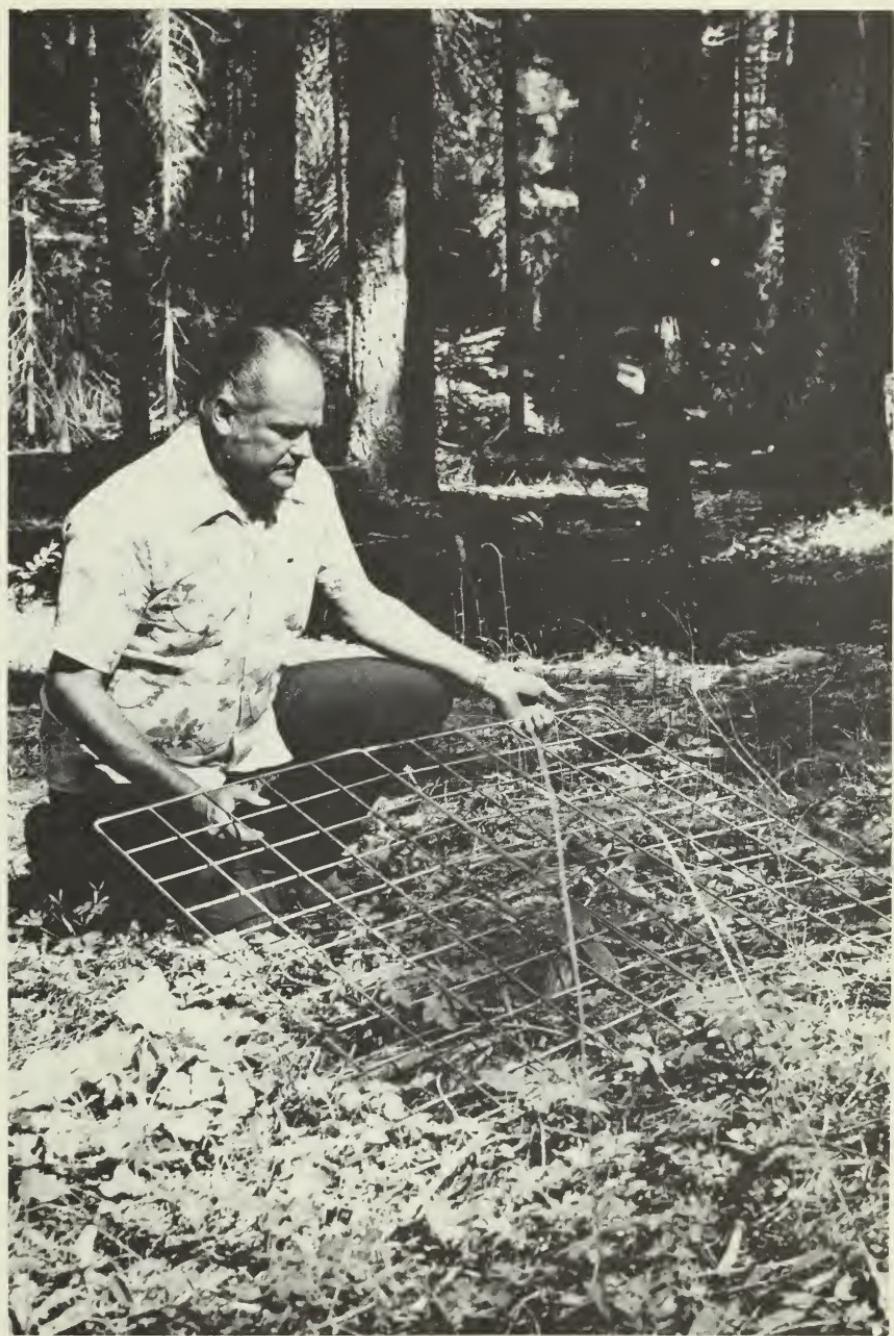


Fig. 17. Meter square grid being used by Tom Harvey.

monitored in both the treated sections and the controls in order to ascertain the relative effects of the manipulation and fire.

An inventory of tree species was taken in both treated and control sections in addition to the surveys of ground species of herbs and shrubs. Particular interest centered on white firs and giant sequoias, as they are respectively considered to be climax and disclimax dominants in those areas where physical factors permit giant sequoias to grow. Harlow and Harrar (1969) listed the tree species that occur in the study areas with respect to the conditions of shade tolerance as follows: giant sequoia and ponderosa pine, intolerant; sugar pine and incense cedar, intermediate or cedar may also be considered to be tolerant; and white fir, tolerant. It was hypothesized that if fire favors giant sequoias they should show relatively better survival and growth than white firs in the manipulated sections in comparison to the control sections.

### *Methods and materials*

In order to assess vegetational changes following manipulation, a series of permanent plots was established in the study areas (Mueller-Dombois and Ellenberg 1974). For ground vegetation analysis 2 m<sup>2</sup> plots were established in both treated and control areas. They were surveyed as to number and species of plants less than a meter in height prior to treatment, one year after treatment, three or four years after, and eight or nine years after treatment. A one meter square grid marked off in square decimeters was used to facilitate location and counting of plant species (Fig. 17).

Permanent regularized plots measuring 5 m x 20 m were established in three areas for assessing tree vegetation greater than 1 m in height. These plots were examined prior to manipulation, and the treated sections were surveyed one year after manipulation and fire, and both types of sections were surveyed again in 1974. In addition tree populations were assessed by the random pairs method (Phillips 1959) in all but North Area. Trees were selected and measured as to distance apart, species and diameter at breast height. In 1974 a complete survey of snags was made in all study areas, and a comparison made as to species, size, and abundance in treated versus control sections.

### *Results*

Light determinations were made at 114 2 m<sup>2</sup> ground vegetation plots, thus making an analysis of levels of relative capacity to tolerate shade by some plants possible (Figs. 18-20). Each bar representing percent expected was determined by dividing the total number of sample plots into the number of plots that had a given light value; e.g. 60% of the sample plots had sunlight values of 0-9%. The abundance and frequency percentages

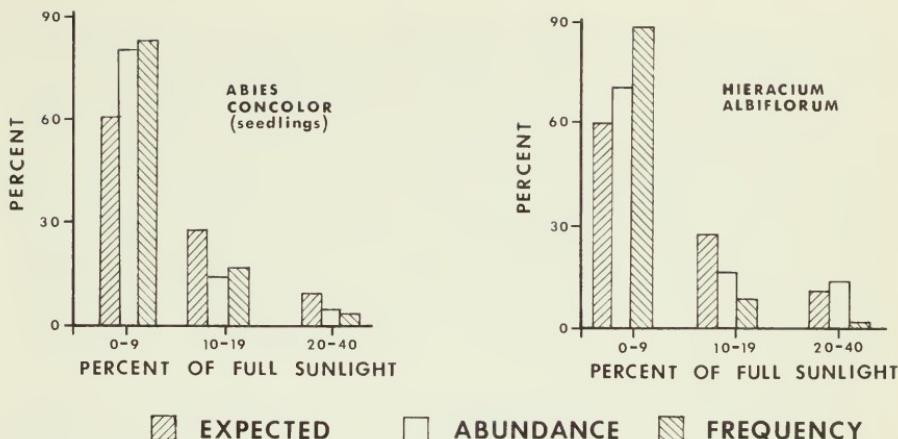


Fig. 18. Plant response in 114 plots to percentage of full sunlight (explanation in text).

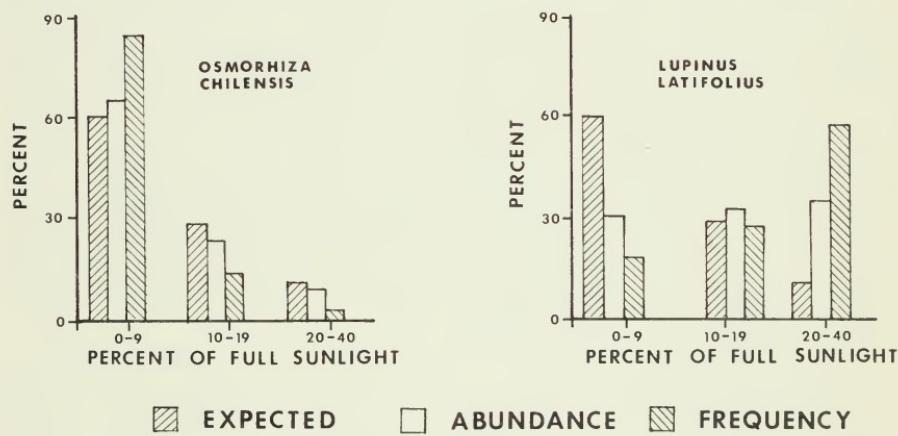
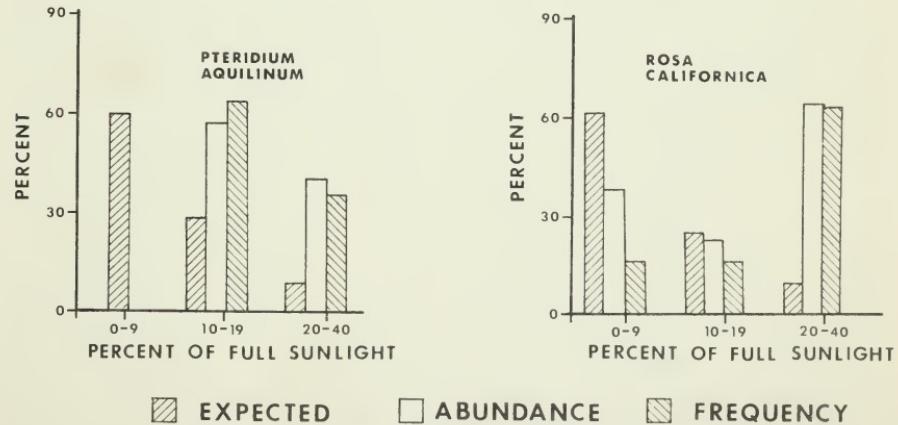


Fig. 19. Plant response in 114 plots to percentage of full sunlight (explanation in text).



of various species are based on the relative occurrence of a species population in plots with given light values. For example, of all the white firs in sample plots, 82% are in plots with 0–9% of full sunlight. Therefore one can contrast what might be expected if a plant was distributed independently of sunlight values with its actual distribution. From the graphs (Figs. 18 and 19) it is evident that *Abies concolor*, *Hieracium albiflorum* and *Osmorhiza chilensis* had higher frequencies and levels of abundance in the low categories than there were plots with those light intensities. *Galium triflorum*, *Pyrola picta* and *Adenocaulon bicolor* had similar responses, with more than 20% higher values for abundance and/or frequency in the 0–9% full sunlight category.

*Lupinus latifolius*, *Pteridium aquilinum* and *Rosa californica* were under-represented in the low light plots and over-represented in the higher lighted plots (10–40% full sunlight). Two plant species, *Galium sparsiflorum* and *Viola lobata* were more intermediate in their occurrence with respect to light levels. It is of interest to note that the two *Galium* species occur in the same habitat, but that the species with more leaves at the nodes (*G. triflorum* with six leaves) is apparently more shade tolerant than the species with fewer leaves (*G. sparsiflorum* with four leaves).

Light determinations were made in the dense stand of giant sequoia seedlings in Trail Area by randomly placing ten test vials at the site. An average of 13.6% of full sunlight was obtained with a range in values of 10% to 16%. Measurements were also made at locations of individual sequoias, and a correlation coefficient calculated with respect to height. The results are discussed in Chapter 5.

Most (64%) of the litter and duff plots were in the 2–6 cm deep categories. No plants were found in litter and duff greater than 8 cm (3.2 in) deep, however the sample size was too small to draw any inferences. All but *Abies concolor* had percent frequency of occurrence less than expected in the 6–8 cm class (Figs. 21–23). Expected frequency and abundance percentages were calculated in the same manner as for light described above. *Adenocaulon bicolor*, *Hieracium albiflorum*, *Osmorhiza chilensis*, and *Pteridium aquilinum* had higher than expected percentages of their abundance and/or frequency in the thinner duff-litter classes, i.e. in 0–2 cm and 2–4 cm classes. Both *Abies concolor* and *Pyrola picta* appear to be able to tolerate the deeper litter-duff thickness (Fig. 23), as they were at or below the expected percentage in the 0–2 cm class and not at or above the expected percentage in the 4–6 cm class. The annuals *Cryptantha affinis*, *Gayophytum nuttallii* and *Montia gypsophiloides* were found only in the 0–2 cm litter-duff class, which implies an intolerance to thick duff.

The ground vegetation in the different study areas varied slightly in the ranking of abundance and frequency of occurrence of the various species present. It also showed minor variation from year to year, especially in the treated sections. A listing of the treated section in one of the areas

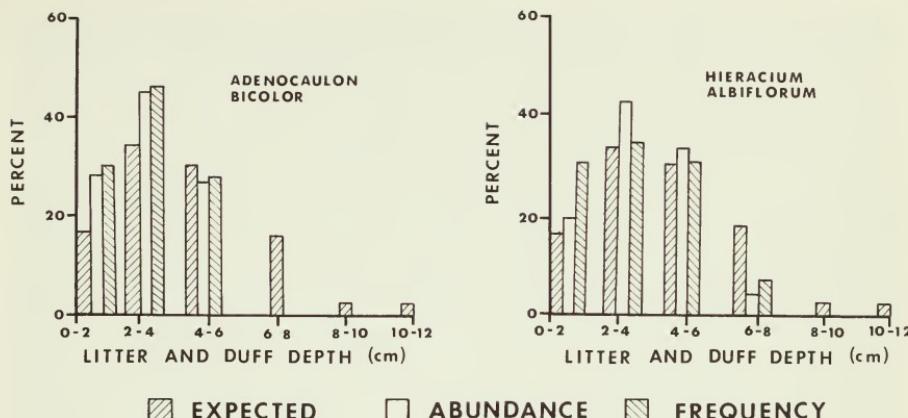


Fig. 21. Plant growth versus litter and duff thickness (explanation in text).

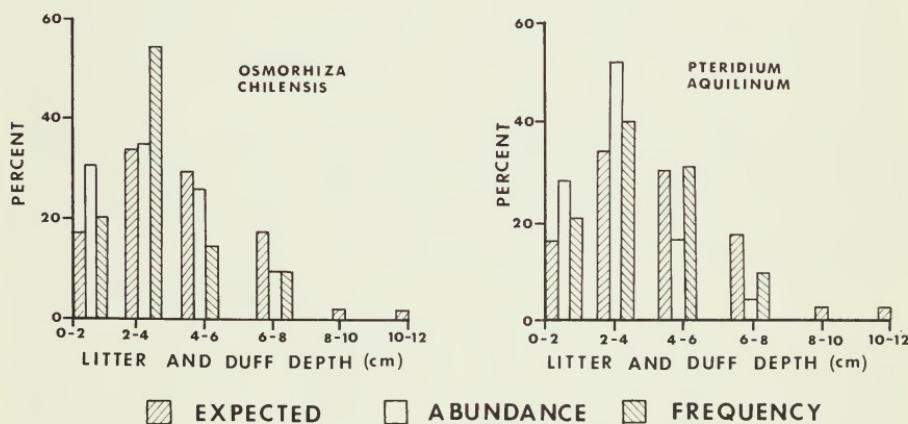


Fig. 22. Plant growth versus litter and duff thickness (explanation in text).

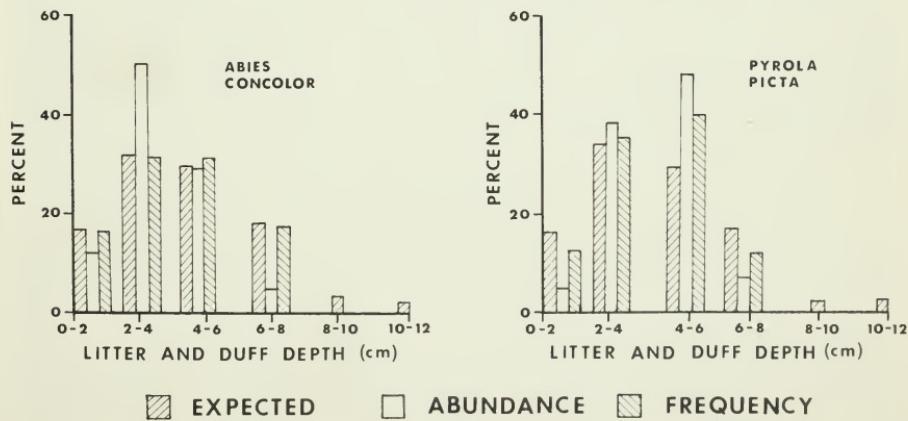


Fig. 23. Plant growth versus litter and duff thickness (explanation in text).

(North Area) prior to treatment indicates the relative importance of most of the plant species (Table 4). A listing of all plant species observed in the study areas is in Appendix I. Voucher specimens are in the San Jose State University Herbarium.

Some of the results from the monitoring of the ground cover vegetation (tracheophytes less than 1 m tall) before and after manipulation are presented graphically in Figs. 24-33. From these graphs it is apparent that certain species show similar response patterns. For example, several annuals that increased significantly following treatment were practically gone seven to ten years after manipulation. Specifically, *Cryptantha affinis*, *Gayophytum nuttallii* and *Gilia giliodes* were never found in the control plots of any of the areas, but increased from zero in number in the manipulated plots of North and Ridge Areas the year or two after manipulation. They then disappeared, or, as in the case of *G. giliodes*, were reduced in number during the seven years after the treatment. The other two study areas (Trail and Ridge) were apparently unfavorable to growth of annuals, possibly being either too dry or having an inadequate seed source.

Certain perennial and biennial plants showed a pattern of population numbers similar to the annuals. They were lacking in the control section plots throughout the study and treatment plots prior to disturbance. In the fire or manipulated plots both types increased dramatically following manipulation or fire, and then gradually decreased. This was especially well documented in the case of *Ribes roezlii*. For example, 12 plants were present in the 10.2 m<sup>2</sup> treated plots of Ridge Area a year after the fire, while nine years later only one plant had survived. Larger populations of *R. roezlii* in the other study areas showed a similar pattern (Figs. 25, 30). *Phacelia mutabilis* responded in a similar fashion (Figs. 26, 31). Other species responded in various ways, as will be discussed below.

The genus *Ceanothus* was represented by only a few individuals in the study areas prior to manipulation and fire. Three species were present, namely *C. integerrimus*, *C. parvifolius* and *C. cordulatus*. Only the first two species occurred in sampling plots in South Area. At this lower elevation site *C. integerrimus* increased from one during pretreatment to 207 in 1974 in the same plots. *C. parvifolius* increased in the same interval from three individuals to a sample population of 1399, and a 50% frequency level. *C. parvifolius* was also observed growing on the perimeters of the burn piles in North Area in the summer of 1965 after the piles had been burned the previous September. A total of twenty-seven plants were observed at the edges of 10 of the 26 burn piles.

The apparent response to treatment of *Lupinus latifolius* var. *columbianus* was of special interest in North Area. Prior to manipulation in 1964 this species covered approximately 40% of the section to be treated. Ten years after fire and manipulation the lupine cover was about 90%.

The fluctuations of those plant species already in fair number in the areas prior to fire and manipulation were less clear in the response after treatment. The three species of greatest abundance were *Hieracium albiflorum*, *Adenocaulon bicolor* and *Osmorhiza chilensis* (Figs. 27, 28, 33). *Hieracium albiflorum* apparently responded by a rapid decrease the year after treatment, but quickly recovered, and in four or five years had returned to population numbers equal to those of pretreatment conditions. *Osmorhiza chilensis* remained at essentially equal levels in the control and treated sections in North Area (Fig. 28). However, in the other three areas there was a significant decrease of populations in the manipulated plots a year after manipulation, as they dropped by about 72%, while control populations only dropped about 22% in abundance. Total population in the control plots was 462, which dropped to 361, while in the treated plots the total population dropped from 515 to 147 after treatment. At the last assessment in 1974 the total inventories were very similar between treated and control plots.

Tree vegetation over 1 m (3.2 ft) in height was found to consist mainly of white fir. Data combined from all four areas indicate that 76.5% of all conifers were white fir, 13.7% were sugar pines, 6.6% were giant sequoias, and 3.0% were incense cedars. In North Area the population of white firs in the treated section was reduced 93%, from 1,010 to 66 per hectare, after 10 years. During the same period the control section had apparently decreased by 21%, from 1,030 to 811 per hectare. The density of white firs was essentially the same for the treated and untreated sections prior to treatment, i.e. 1010 and 1030 per hectare respectively.

In the complete survey of all study areas, dead trees larger than 6 inches dbh were counted. The comparison between treated and control sections was significant. Over twice as many trees were dead per hectare in the treated sections as in the control sections. Of the 115 dead trees 103 were *Abies concolor*, nine were *Pinus lambertiana*, two were *Calocedrus decurrens*, and one was *Sequoiadendron giganteum*. Seven of the *P. lambertiana* were in the control sections and two trees were in the manipulated section. Both dead *C. decurrens* trees were in a manipulated section and the giant sequoia was in a manipulated section. Analysis of the 103 dead white fir (*Abies concolor*) revealed a mortality rate 2.1 times as high in the treated sections as in the control sections (Table 5).

When plotted by size class, the populations of trees showed a difference in the proportion of small versus large individuals (Fig. 34). The treated sections had a greater number of large individuals that had died than the control sections. This was particularly true of the three sections in which heavy equipment had been used. It is possible that mechanical damage occurred, and subsequent invasion by insects or pathogens increased mortality beyond what could be expected from fire alone.

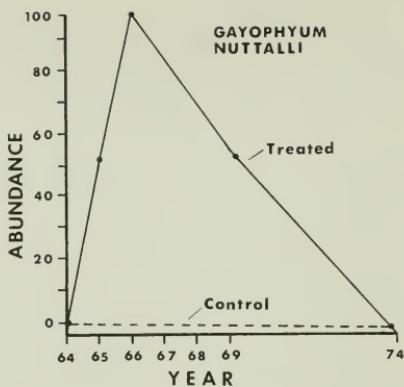
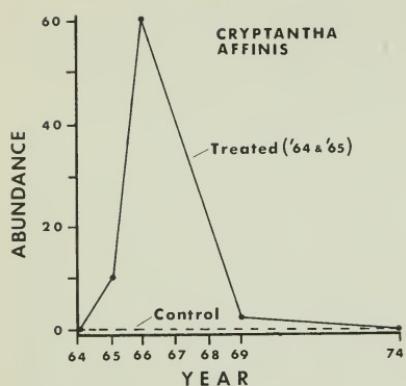


Fig. 24. Plant numbers in 52 2 m<sup>2</sup> plots in response to treatments in North Area in 1964 and 1965.

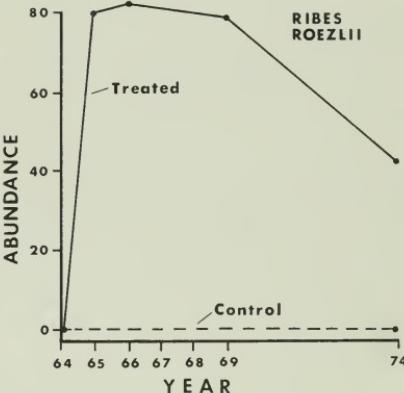
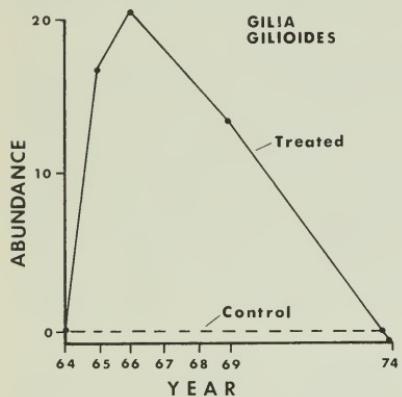


Fig. 25. Plant numbers in 52 2 m<sup>2</sup> plots in response to treatments in North Area in 1964 and 1965.

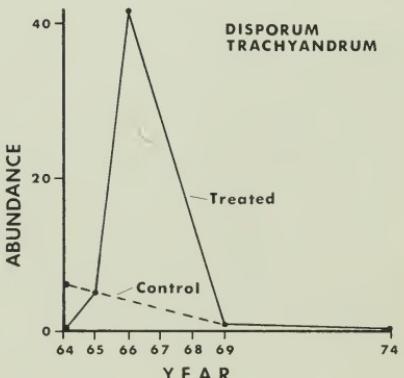
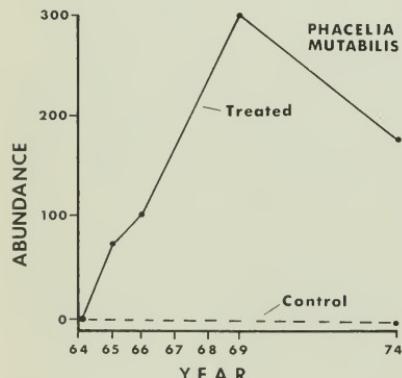


Fig. 26. Plant numbers in 52 2 m<sup>2</sup> plots in response to treatment in North Area in 1964 and 1965.

**Table 4.** Relative importance of ground plant species in North Area.

Species	Relative Abundance (% of total ind.)	% Frequency (% of total)	Mean Density (No./m <sup>2</sup> )
<i>Lupinus latifolius</i> var. <i>columbianus</i>	20	50.0	2.4
<i>Hieracium albiflorum</i>	15	42.8	1.9
<i>Viola lobata</i>	13	71.4	1.6
<i>Rosa californica</i>	11	32.1	1.4
<i>Osmorhiza chilensis</i>	8	46.4	0.9
<i>Silene bridgesii</i>	4	3.5	0.5
<i>Fyrola picta</i>	3	25.0	0.4
<i>Pteridium aquilinum</i>	3	14.2	0.4
<i>Galium triflorum</i>	2	10.7	0.3
<i>Viola purpurea</i>	2	7.1	0.3
<i>Adenocaulon bicolor</i>	1	14.2	0.1
<i>Gayophytum Nuttallii</i>	1	3.5	0.1
<i>Smilacina racemosa</i> var. <i>amplexicaulis</i>	1	10.7	0.1
<i>Viola Sheltonii</i>	1	7.1	0.1
<i>Potentilla glandulosa</i>	1	7.1	0.1
<i>Castanopsis sempervirens</i>	1	3.5	0.1
<i>Draperia systyla</i>	1	3.5	0.1
<i>Disporum trachyandrum</i>	1	3.5	0.1
<i>Goodyera oblongifolia</i>	1	3.5	0.1
<i>Habenaria unalascensis</i>	1	3.5	0.1
<i>Phacelia mutabilis</i>	1	3.5	0.1
<i>Rubus leucodermis</i>	1	3.5	0.1
<i>Ribes Roezlii</i>	1	3.5	0.1
<i>Symporicarpos mollis</i>	1	3.5	0.1

**Table 5.** Mortality of *Abies concolor* (6" dbh) in manipulated versus control section, eight to nine years after manipulation.

Area	Number of dead <i>A. concolor</i> per hectare	
	Manipulated	Control
Trail	16	9.8
Ridge	18	2.5
North	12	7.2
South	6	1.8
Mean	12.5	5.9

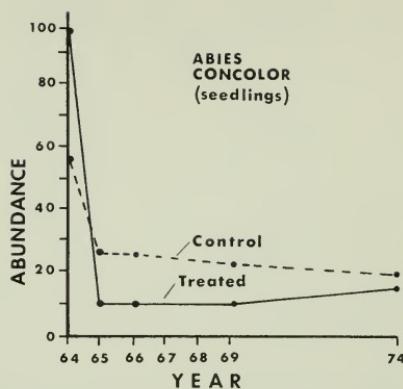
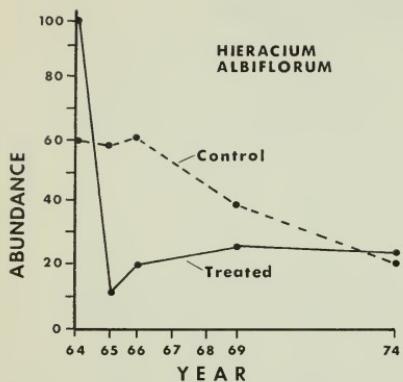


Fig. 27. Plant numbers in 52 2 m<sup>2</sup> plots in response to treatment in North Area in 1964 and 1965.

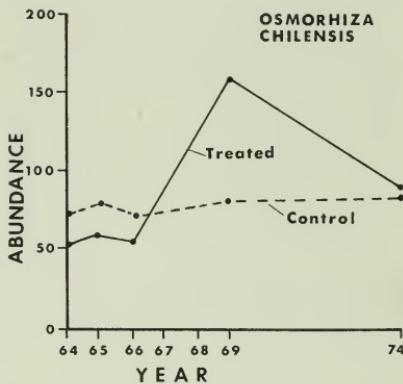
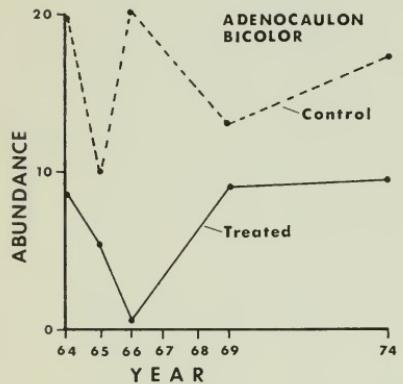


Fig. 28. Plant numbers in 52 2 m<sup>2</sup> plots in response to treatment in North Area in 1964 and 1965.

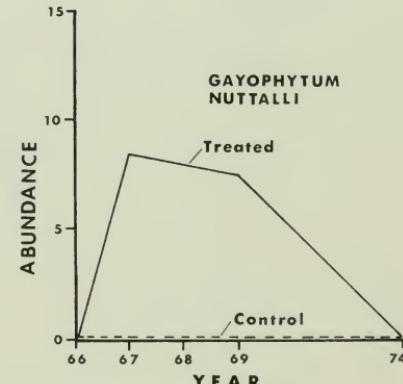
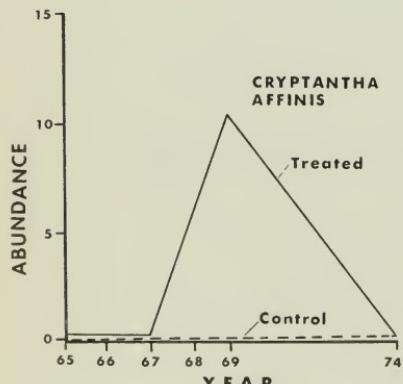


Fig. 29. Plant numbers in 37 20 m × 1 cm transects in response to treatment in South Area in 1966.

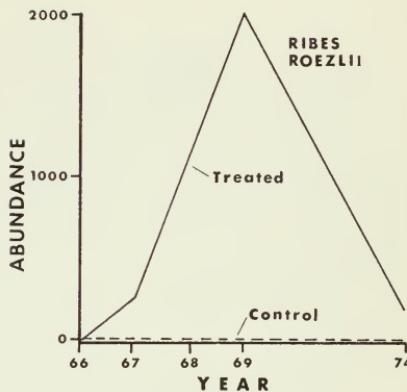
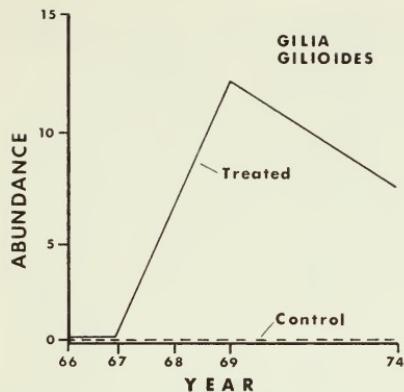


Fig. 30. Plant numbers in 37 20 m × 1 cm transects in response to treatment in South Area in 1966.

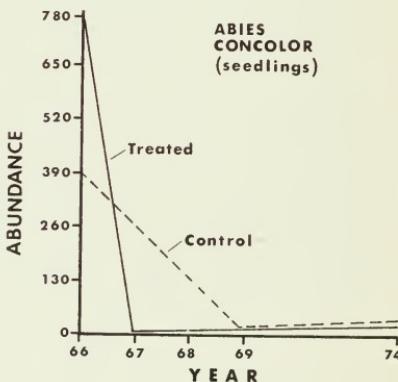
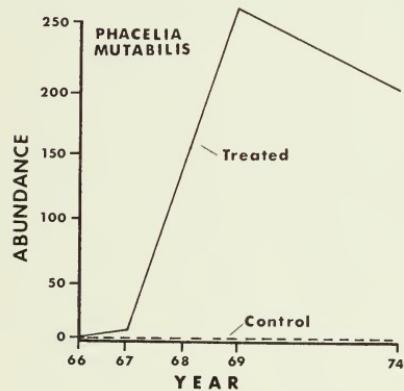


Fig. 31. Plant numbers in 37 20 m × 1 cm transects in response to treatment in South Area in 1966.

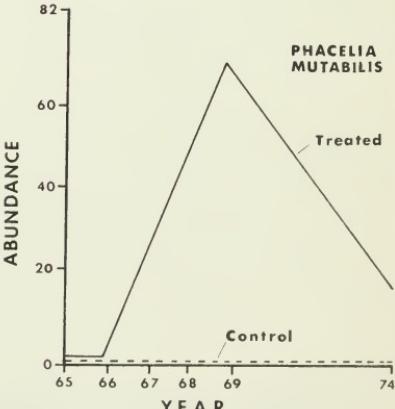
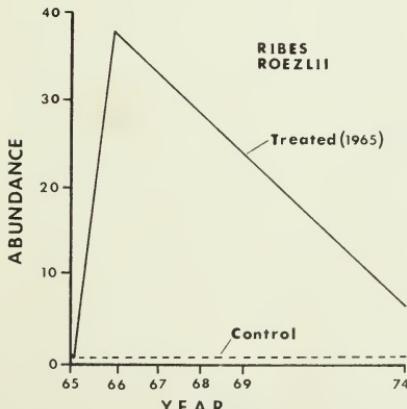
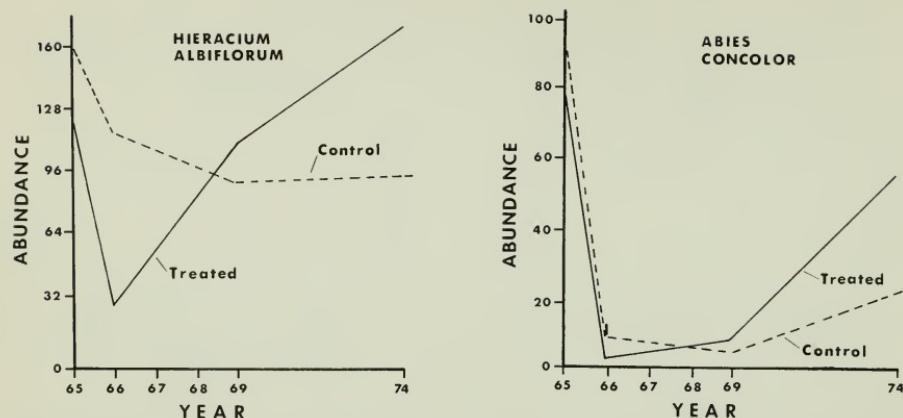
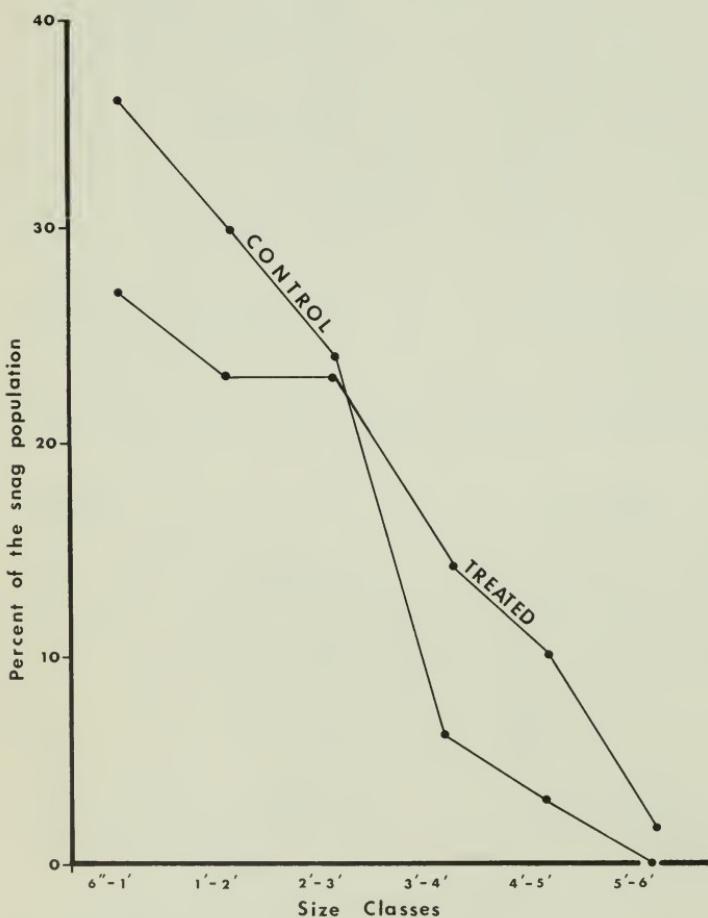


Fig. 32. Plant numbers in 41 2 m<sup>2</sup> plots in response to treatment in Trail Area in 1965.

Fig. 33. Plant numbers in 41 2 m<sup>2</sup> plots in response to treatment in Trail Area in 1965.Fig. 34. Mortality of *Abies concolor*, snags by size class in treated versus control sections.

## Discussion and summary

In light of the patchiness of heat intensities and other irregular factors during surface fires, it is not surprising to find a patchiness in subsequent reproduction of various plant species. Temperatures favorable to seed germination of shrub species, such as *Ceanothus* spp., will increase their numbers in certain spots, while high temperatures will reduce them. Kilgore and Biswell (1971) reported 16,000 deerbrush (*Ceanothus integrifolius*) seedlings per hectare on a lightly burned section and only 540 seedlings per hectare on a heavily burned portion, while no seedlings appeared on unburned control plots. The increased number of *Ceanothus* spp. after fire becomes ecologically important since these nitrogen-fixing shrubs contribute to the chemical nature of the soil (Kilgore 1973).

Two species of the same genus (*Galium*) appear to have different light requirements and may be adapted by leaf number to their special spectrum of this physical environmental factor. The one that occurs in less light has more leaves.

In a forest successional series, white fir is generally accepted as a late stage tree and tolerant of shade. The present studies quantify this contention and indicate that white fir was most abundant at the lower sunlight values of less than 9% full sunlight, and in fact it was most frequent in plots at only 4% full sunlight. Other species such as *Pteridium aquilinum* and *Rosa californica* had high relative frequency and abundance values in plots from 20% to 40% full sunlight, while others such as *Viola lobata* and *Galium sparsiflorum* were intermediate.

In addition to tolerating the lower light values of later successional stages, white fir was also quite tolerant of relatively deep duff and litter. On a basis of frequency of occurrence, white fir was present at near expected percentages, whereas several other species, e.g. *Adenocaulon bicolor* and *Hieracium albiflorum*, were underrepresented in the thicker litter and duff categories of 6–12 cm in depth, although sample size was insufficient to draw firm conclusions.

There was an increase of annuals in the treated sections of two study areas following the fires or manipulation. After 10 years, however, they were no longer present. This would seem to suggest that ground conditions quickly become unfavorable for germination and/or seedling survival for this type of plant. The fact that none was found where more than 2 cm of litter had accumulated indicates one such condition. Giant sequoia also appear to be a species for which conditions are optimal for only a few years following fire or manipulation (see Chapter 5).

The shrub stage in succession was represented by several species, particularly members of the genera *Ceanothus* and *Ribes*. They, along with *Phacelia mutabilis*, showed a rapid increase after fire and manipulation and then a subsequent decline in numbers. Although they appear

to be approaching the population levels pertaining prior to the experimental treatment, it probably will require a few more decades. In a second-growth giant sequoia forest about 1.8 kilometers (1 mi) west of our study area Biswell et al. (1966) suggested that the shrub phase was essentially terminated about 40 to 50 years after logging and fire disturbances in the late 1800s. By 1966 at that site, most shrub species were at less than 5% frequency, while only two shrub species were in the 10% to 20% frequency category (Biswell et al. 1966). In our study areas the relatively rapid passage of annual herbaceous species and of shrub species may be due in large part to the minor alteration in the canopy cover which apparently induced only modest increase in sunlight at the ground level.

In a survey of both control and manipulated sections (with total area of about 11.5 ha) it was discovered that since treatment, twice as many white fir had died in the fire and manipulated sections as in the control sections. In addition there was a disproportionately larger number of large firs that died. More trees in the 1.8 m to 3.6 m (3 ft to 6 ft) classes, which were about 250 years old, died in the manipulated sites than on the non-manipulated. Thus, after about a decade, openings were being created in the crown canopy. This is in contrast to Kilgore's (1973) findings, where only the young firs were affected. Therefore, if another prescribed burn was soon applied to the study areas, the ground conditions might become favorable once again to early stage plants and thus more nearly approximate the space-time mosaic considered by Bonnicksen (1975) as characteristic of this forest ecosystem.

# Giant Sequoia Reproduction, Survival, and Growth

H. Thomas Harvey

## Introduction

In order for forest trees to perpetuate themselves they must not simply produce seeds in sufficient number, but the seeds must germinate and the developing seedlings must be able to tolerate the environmental conditions into which the seeds have fallen. Thus, extant species have evolved a variety of strategies to insure adequate seed production and subsequent survival of offspring. In terms of its strategy of seed production that involves serotinous cones, the giant sequoia differs dramatically from other members of the Taxodiaceae. The other members of the family produce cones that normally shed their seeds in less than two years after starting development (Buchholz 1938). Giant sequoia cones start forming in the summer of a given year and are pollinated the following spring. Fertilization takes place by that fall, and the cones mature the following summer (Buchholz 1937), thus the whole process takes more than two years. These serotinous cones may remain green and closed for over twenty years (Buchholz 1938). The giant sequoia is dependent on the seeds from these mature cones for its sole method of reproduction. Although its closest living relative, the coast redwood (*Sequoia sempervirens*), is noted for propagation through stump sprouting (Stebbins 1948), no sprouts from roots or stumps are known to occur in the giant sequoia (Schubert 1962).

These two native California sequoias also differ markedly in the number of seeds per cone. The coast redwood yields only about 60 seeds per cone while the giant sequoia cone averages about 200 seeds (Buchholz 1939). Slightly higher averages of seeds per cone have been reported for the giant sequoia, namely about 230 (Schubert 1962) and 234 (Fry and White 1930). Both of these latter sources report a maximum of 329 seeds per cone, thus the average number of about 230 seeds per cone reported by Schubert (1962) may be based on the Fry and White (1930) determinations. Schubert (1962) reported that the seeds fall at a rate of about 120 cm/sec (4 ft/sec) and may be blown laterally as much as 177 m (580 ft). This would enable the groves to gradually expand, providing conditions on the periphery are favorable for seed germination and seedling survival.

The number of cones produced per tree has been reported by Schubert

(1962) to be 2000 per year for mature trees. The total number of cones on a large mature tree that fell in Whitaker's Forest was estimated to be about 50,000 (Zinke pers. comm.). At what age trees first produce cones with germinable seeds is still uncertain, with Schubert (1962) reporting that trees about 20 years old produced infertile seeds.

Although cones may remain closed for over 20 years, natural forces may open them before then. Douglas squirrels have long been known to feed on the cones and thus may release seeds in the process (see Chapter 9). The convective movement of hot air in hot surface fires may dry cones and cause heavy seed fall. Kilgore and Biswell (1971) reported that hot air rising to about 36 m (100 ft) during a prescribed burn on Redwood Mountain dried numerous cones which subsequently released many seeds.

Although most tree species have some kind of seed dormancy (Kramer and Kozlowski 1960), the giant sequoia seeds germinate as soon as conditions are favorable. Those seeds falling on litter and humus are usually unable to establish seedlings (Metcalf 1948). Stark (1968b) reports that litter, if wet, is a good germination medium but in nature litter rapidly dries out, thus desiccating the seed or seedling dependent upon it. This is in contrast with most coniferous seeds which can tolerate air-dry conditions (Kramer and Kozlowski 1960).

Hartesveldt and Harvey (1967) reported giant sequoia seeds on the ground after a prescribed fire at a concentration of 7,500 per m<sup>2</sup>. This high concentration was attributed to the heating of the cones of a large sequoia near an adjacent burn pile.

Seed germination of the giant sequoia begins in February or March and proceeds throughout the summer as long as conditions are suitable (Schubert 1962). Giant sequoia seeds germinate best in moist soil about 1 cm below the surface, at 10°C to 20°C, pH 6 to pH 7, and reduced light (5,000 f.c.) (Stark 1968b). Stark also reported that selected large seeds (8 mm average length) germinated 153% better than a mixture of normal seeds, while small seeds (under 4 mm average length) germinated only 6.9% as well as the controls.

Seed germination is highly variable even when seeds are treated to the best of conditions. Stark (1968b) tested 12,000 seeds from 42 sequoia groves and obtained an average of 22.5% germination. The highest germination she obtained was 55.5%. Metcalf (1948) obtained 42% germination from seeds removed from an old lichen covered cone. Fry and White (1938) reported that 15% germination was a fair average, but estimated that only one in a million seeds germinates under natural conditions.

Hartesveldt and Harvey (1967) reported that all test seeds scattered on the surface of the forest floor in a sequoia grove failed to germinate after 20 days exposure. They further stated that under conditions produced by surface fires, soil surface temperatures may be as high as 48.9°C (120°F)

to 69.4°C (157°F), which would rapidly desiccate the seeds and the seedbed.

The microenvironment of the forest ground surface first influences seed survival, then germination, and upon germination, the development and survival of the seedlings. The early seedling stage is probably one of the most critical as far as the survival of the species is concerned. Hartserveldt and Harvey (1967) followed over 2,000 seedlings which had naturally seeded in after the prescription burning of two test plots. At the end of the first summer 45% were alive. By the end of October, 30% remained alive, and by the next summer only 10%. Only 1.4% of the seedlings were still alive after two summers of growth, thus in 18 months 98.6% mortality had occurred.

Fire is among the physical factors that are considered beneficial to sequoia seedling survival through indirect means. Large trees such as white fir may be killed, thus opening up the canopy and letting in additional light which is required by the seedlings. Also the soil may be affected in several ways.

If the temperature is lethal to seeds buried in the soil, then potential competitors to the giant sequoia seedlings will be eliminated. High temperatures make the mineral soil friable and wettable (Donaghey 1969). Friable soil allows falling sequoia seeds to penetrate, particularly during a rain storm. Wettability was observed by Donaghey (1969) to increase with increased temperature, and thus it allows greater water penetration. Friable soils may allow easier root penetration and thus enhance the establishment of young seedlings.

High temperatures from hot fires may also eliminate potential pathogens such as *Penicillium* sp. which produces necrosis of the hypocotyl in giant sequoia seedlings (Swift, W. 1975). Bega (1964) reported several fungi as potential pathogens of seedlings. Heat may also volatilize any ectocrines that may be present. Therefore if any or all of the above are true, then giant sequoia seedlings should survive best where the hottest fires have occurred, provided the fires do not destroy the seed source. One favorable factor that may be adversely affected by hot fires is the endomycorrhizal fungi associated with giant sequoia. S. Swift (1975) found that seedlings could survive for at least 3 months under sterile conditions without mycorrhizae and thus may survive until mycorrhizal relationships are established. Many conifers require mycorrhizae for survival, and the giant sequoia does not appear to be an exception.

### *Grove expansion and longevity of remnants*

The giant sequoia is considered a relict species which persists in relatively restricted groves at the mid-elevations in the Sierra Nevada (Hartserveldt 1962). Rundel (1971, 1972a) has stated that there is no evidence

of any change in grove boundaries during the last 500 years or longer. No remnants of sequoias between the present disjunct populations have been found, although individuals or only a few trees exist a kilometer or so beyond the closest grove. There is a lone 150 year old tree, for example, at Rabbit Meadow over a kilometer north of Redwood Mountain Grove.

The question of how long downed giant sequoia may persist is related to the above question of grove expansion or contraction. If dead giant sequoias may persist standing for over 2000 years, as determined by Hertesveldt (1964), then evidence should be available to infer grove contraction in this case.

## *Methods and materials*

### *Seed production*

Four major aspects of seed production were examined. These were 1) the number of mature trees producing cones per hectare, 2) number of cones per tree, 3) number of seeds per cone, 4) and number of, and timing of, seeds reaching the ground.

The number of trees per hectare was determined by mapping all giant sequoias in the study areas. In addition, two surveys by commercial forestry companies for the National Park Service of the Redwood Mountain Grove and the Giant Forest were analyzed to determine the density of mature giant sequoias.

The number of cones per tree was estimated by two methods. Stecker (Chapter 7) hand-counted cones within the crown of the 88.4 m (290 ft) Castro Tree. Using binoculars from the ground, Shellhammer (Chapter 9) devised a cone load system for estimating cone numbers in mature trees.

The number of seeds per cone was determined by taking individual cones and placing them either in small paper bags and allowing them to air dry, or placing them in aluminum foil and oven-drying them. After drying, each cone was examined, any remaining seeds were teased from the cone, and then all seeds were counted. Almost 200 cones were examined in this fashion. Additional data were gathered on number of scales per cone, size of cone and variation between trees as to the number of seeds per cone.

The number of seeds falling per unit was determined by placing 29 catch panels each  $1\text{ m}^2$  on four transects through North Area. Two  $1\text{ m}^2$  catch panels were placed among 11 large giant sequoias and monitored daily during one summer. On two occasions 10 randomly selected  $\text{dm}^2$  plots were examined for seeds that had fallen to the ground in an apparent heavy concentration.

### Seed germinability

Two methods were employed to determine seed germinability. Seeds were either planted in loamy sand at a depth of 1 cm or placed on moist filter paper in petri dishes. The depth of 1 cm was considered optimal by Stark (1968), and loamy sand is the prevalent type of soil in giant sequoia groves. In addition, the snap test was used to rapidly ascertain whether a batch of seeds appeared to be viable and thus probably germinable.

Perhaps the distinction between viable and germinable needs to be clarified. A seed may be viable but unable to germinate for various reasons when placed under conditions optimal for germination, i.e. alive but unable to germinate. For example, seeds in first year cones are viable (alive) but are not capable of germinating. If a seed did germinate, it of course was viable. In the snap test a seed was snapped (broken) across the long axis of the seed and the condition of the embryonic area assessed. If the area was cream colored and full, it was considered viable and thus potentially germinable. If the area was white, brown or black and/or shrunken, then it was considered nonviable. Parallel tests were run to determine the similarity of results from petri dish or soil germination tests and snap tests.

In order to test the effect of natural environmental conditions on germination, seeds were collected from one seed source and placed on the ground in North Area and thus exposed to natural conditions during the summer. At intervals a sample of 100 seeds was selected for both soil germination and snap test examination to evaluate the effect of light, moisture and temperature.

In order to ascertain the effect of the cone pigment on germination three thousand seeds were tested in five concentrations of the cone pigment, i.e. 22%, 18%, 9%, 4.5%, and 2.2% by weight. The seeds were tested for germination with 10 replicates of 50 seeds each, maintained at 26°C to 30°C in petri dishes.

### Seedling establishment and mortality rates

The period of seedling establishment, as stated earlier, is one of the most critical stages in the life cycle of the giant sequoia. Even though seed germination conditions may be optimal, the species will not survive if the seedlings are quickly decimated. In order to determine the rate of survival and the factors involved, all seedlings that could be found in the treated sections during two or three summers were numbered and staked and then followed as individuals throughout the study. The numbered stakes were placed approximately 10 cm north of each seedling in order to minimize such unnatural effects as shade and root disturbance. During the study period 7,666 giant sequoia seedlings were so marked. The condition of the seedling was noted as to development at the time each was

discovered. Namely, the presence of cotyledons, secondary leaves and branches was recorded, as was the condition of the substrate. Records were kept as to the combination of treatments that may have occurred at the seedling's site, such as scarification due to the heavy equipment, scarification plus surface fire, surface fire alone, or burn pile. In addition, the microhabitat of the seedlings was identified. Seedlings next to fallen twigs or next to rocks were recorded, as was the substrate if it was a standing or fallen rotten log. Hence the mortality that occurred to the seedlings in succeeding years on certain substrates or in certain microhabitats could be evaluated and correlated with such environmental conditions.

Meter wide transects were run in all treated and control areas during the summer of 1969. These surveys, plus random searches for seedling giant sequoias in untreated areas, yielded data which help evaluate the significance of fire and/or manipulation in giant sequoia regeneration. The transects were run in mid-July and then repeated in late August in order to determine the mortality rate.

Mortality rates for the large individualized study of 7,666 seedlings were determined by both weekly and monthly surveys during 1966 and 1967, or by yearly surveys, generally run during the third week in October. During the weekly surveys in 1966 and 1967 each dead giant sequoia seedling was exhumed and analyzed for cause of death. The specimen was then preserved. The weekly determinations of mortality helped define the causes of death. The monthly determination helped identify the period of the year when mortality was greatest. The yearly surveys assisted in determining the annual rate of mortality.

### Growth rate

The growth of trees is a constellation of activities, as suggested by Kozlowski (1962). We concentrated, however, on vertical and diameter growth of individual trees. These measurements were made during three stages in the giant sequoia's life history. Particular interest was taken in the early seedling stage, where height measurements were taken and relative lengths of shoots versus roots were made on exhumed dead seedlings. Height and dbh (diameter at breast height) were measured on sapling-sized trees at Cherry Gap and Converse Basin (Fig. 3) in 1964, 1969 and 1974.

On large trees (over 4 feet in diameter) dbh was taken, and often increment cores were also removed. Increment coring was done on three trees inside each treated section and three trees in each control section in 1974 in order to ascertain the effect of fire and/or manipulation on their respective rates of growth.

## Seedling survival and growth

Several of the factors measured as relevant to succession were also involved in assessing giant sequoia survival and growth. Specific attention was paid to soil moisture and light availabilities using the methods described in Chapter 3. The amount of moisture at the individual sites of certain giant sequoia seedlings was monitored, and a correlation coefficient determined between percent of full sunlight and height of seedlings.

Two projects were carried out involving the association of fungi with giant sequoia seedlings. Methods were developed to grow seedlings in sterile conditions on White's medium and then to inoculate them with fungal isolates. In studies on mycorrhizal relationships, other aseptic seedlings were examined for mycorrhizae and inoculated with isolates from other sequoia roots shown to have endomycorrhizae. The results of these studies are reported briefly in the introduction to this chapter.

## Grove expansion and remnants

Grove expansion was investigated by inspecting the maps of grove inventories and selecting sites where apparently young trees were at the edge of the grove. Increment cores were taken of the suspected young trees and the nearest mature sequoia for age determination by basal area regression and fire history to determine whether the date of a fire correlated with the age of the young sequoias.

To determine the longevity of fallen sequoias, particularly in meadows, cores were taken from trees growing in the root pits of fallen sequoias, and basal area regression curves were used to extrapolate to the beginning of the tree in question.

## Results

### Seed production

The reproductive capacity of a plant that relies entirely on seeds for propagation depends on basic characteristics, e.g. the number of reproductive individuals per unit area. For the giant sequoia, the total density of such trees may be about 37 per hectare. However, if only mature trees greater than 4 ft dbh are considered, the value is significantly lower. The decision to use 4 ft dbh for designating mature giant sequoias was based on several lines of evidence. First, the 4 ft diameter class is the size at which population curves for two large mature giant sequoia groves level off (Fig. 35) and second, this is the diameter of trees about 40 to 86 m (110 to 240 ft) tall and capable of bearing large numbers of cones. As a general rule, a tree that height will be about 400 years old (Fig. 36), and

for the first 800 years of growth the ratio of 1 ft in diameter growth equals 100 years is a reasonable estimate (Fig. 37). After 800 years the radial growth slows so that by 2000 years the average tree measured was 14.5 ft in diameter. (These data were derived from the measurements on cut stumps taken by Huntington in Converse Basin. Copies of his field notes served as the basis of a computer program from which radius and basal area were calculated for each 10 year period on 97 trees.)

Taking mature giant sequoia as ones larger than 4 ft in diameter, and using the tree surveys done in the two largest groves as a basis of density determination, the mean density was 5.3 trees per hectare. According to the surveys, there were 11,890 trees larger than 4 ft in diameter in 2,247 hectares. A comparison of diameters of 19 trees in Trail Area, between our measurements taken above the butt swell and those of the Western Timber Service Tree Inventory of the same trees, revealed a larger value on the average by the latter. The average increase was about 5 inches per tree, which may mean that a few trees may have been included in a class size they should not have been. The discrepancy was least in the small diameter classes. The error introduced by the arbitrary decision of where to take the diameter reading above the butt swell was of little consequence for those about 4 ft in diameter.

Given a mean of 5.3 mature trees per hectare, the next question was how many cones do they produce per tree per year? Through in-tree determinations by Stecker (see Chapter 7) and on-the-ground calculations by Shellhammer (see Chapter 9), we estimated that the typical mature tree may have about 14,000 cones. The number of new cones added per year was estimated to be about 1,500 on the average, although Stecker has counted over 20,000 new cones in the Castro Tree, added in one seemingly exceptional year.

Assuming that a mature giant sequoia puts on approximately 1,500 new cones in the average year, then a basic question is how many seeds are produced per cone? From the 196 cones examined, a total of 39,684 seeds were counted yielding an average of 202.4 seeds per cone with a range of 47 to 393 seeds. The number of seeds per average cone varied significantly from tree to tree (Fig. 38). Earlier disagreements as to the number of seeds per cone may be due to collections of cones all from one tree. If 1,500 new cones per tree are added and there are 5.3 mature trees per hectare and about 200 seeds per cone, then approximately 1,590,000 seeds would be produced annually in a hectare.

Cone scale counts on 183 cones showed a total of 6,136 scales, for an average number of scales per cone of 33.5, and an average of about 6 seeds per scale. This is slightly less than the 36 scales per cone reported by Beidleman (1950). The maximum number of scales per cone reported by him was 56. We found one cone with 61 scales, unusual because all other cones we have examined (several thousand) have a 3/5 Fibonacci

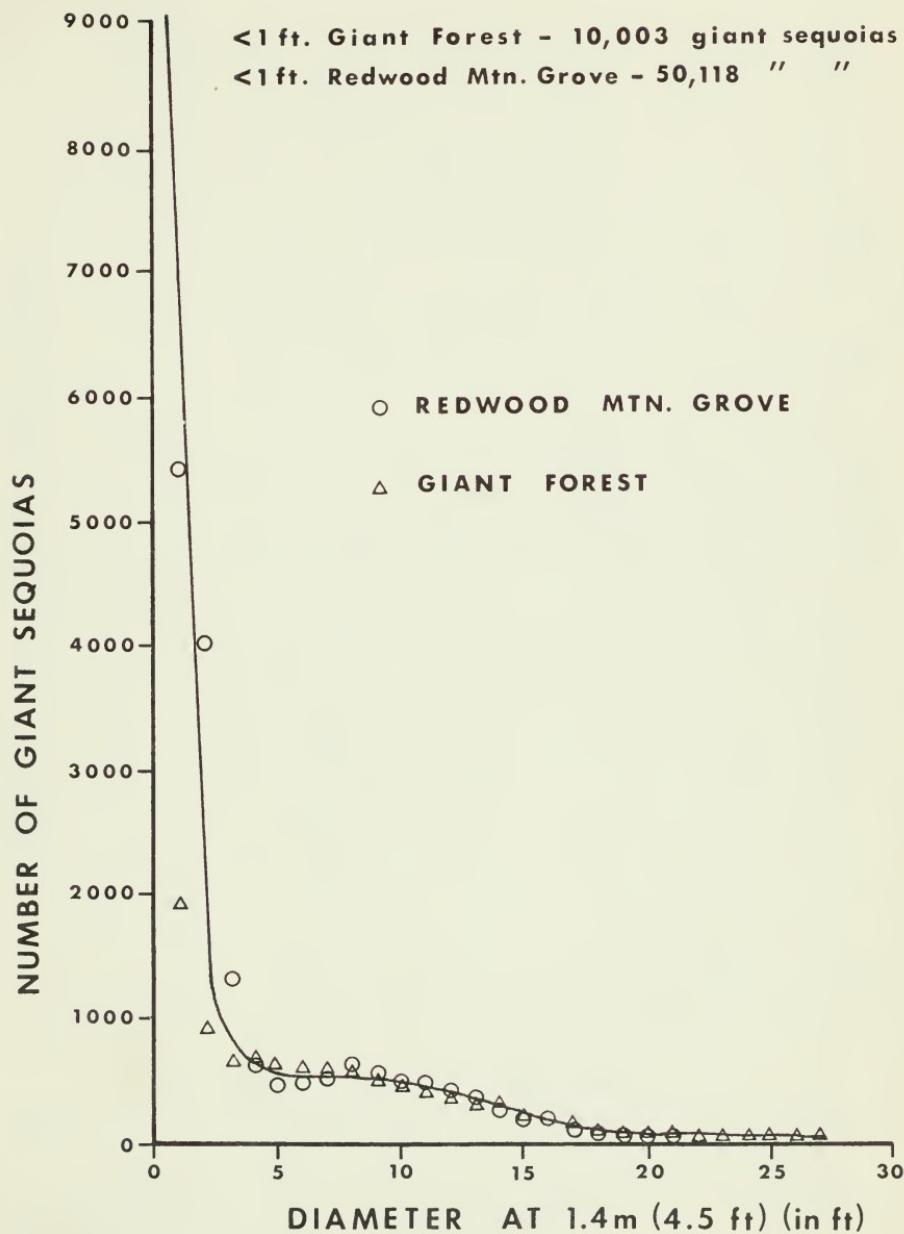


Fig. 35. Number of giant sequoias in two mature giant sequoia groves with respect to dbh.

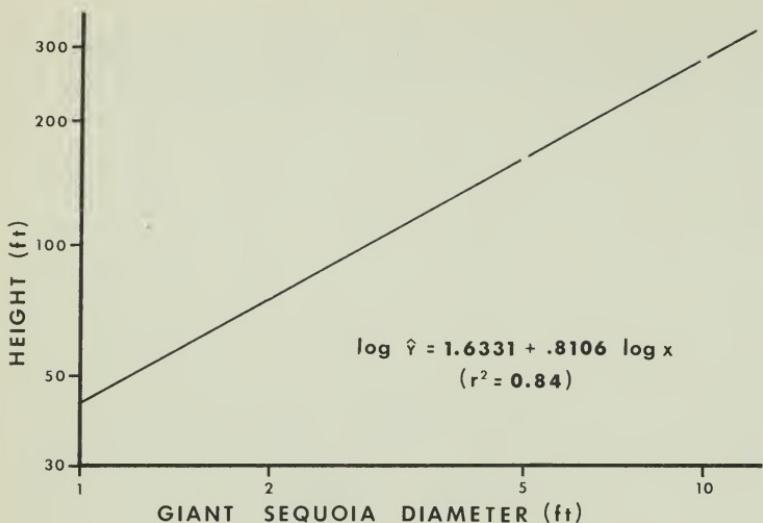


Fig. 36. Regression of height of giant sequoias to diameter (n=227).

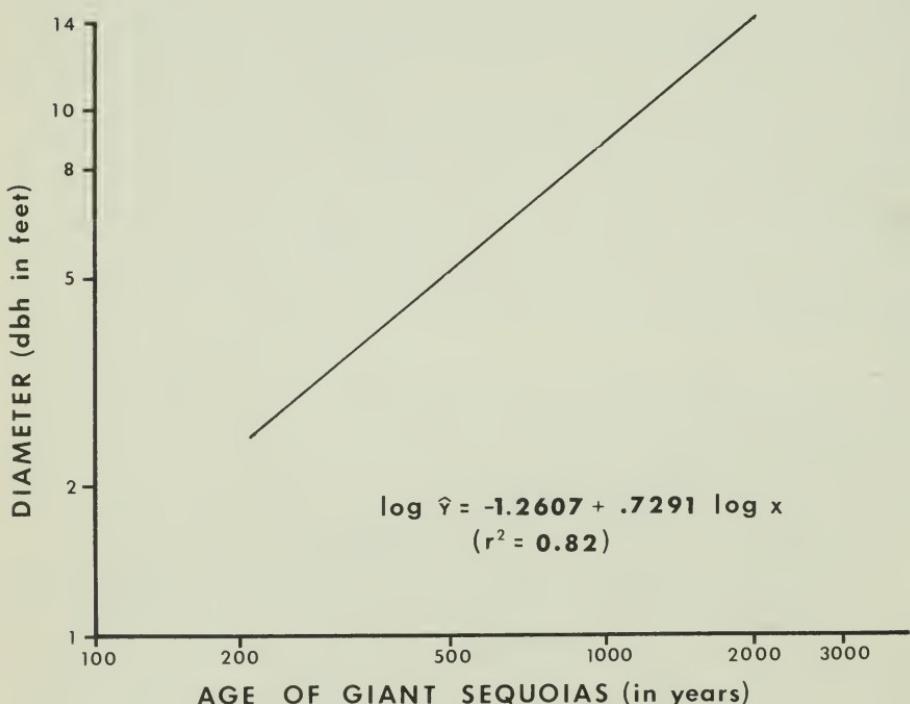


Fig. 37. Regression of diameter of giant sequoias to their age (n=97).

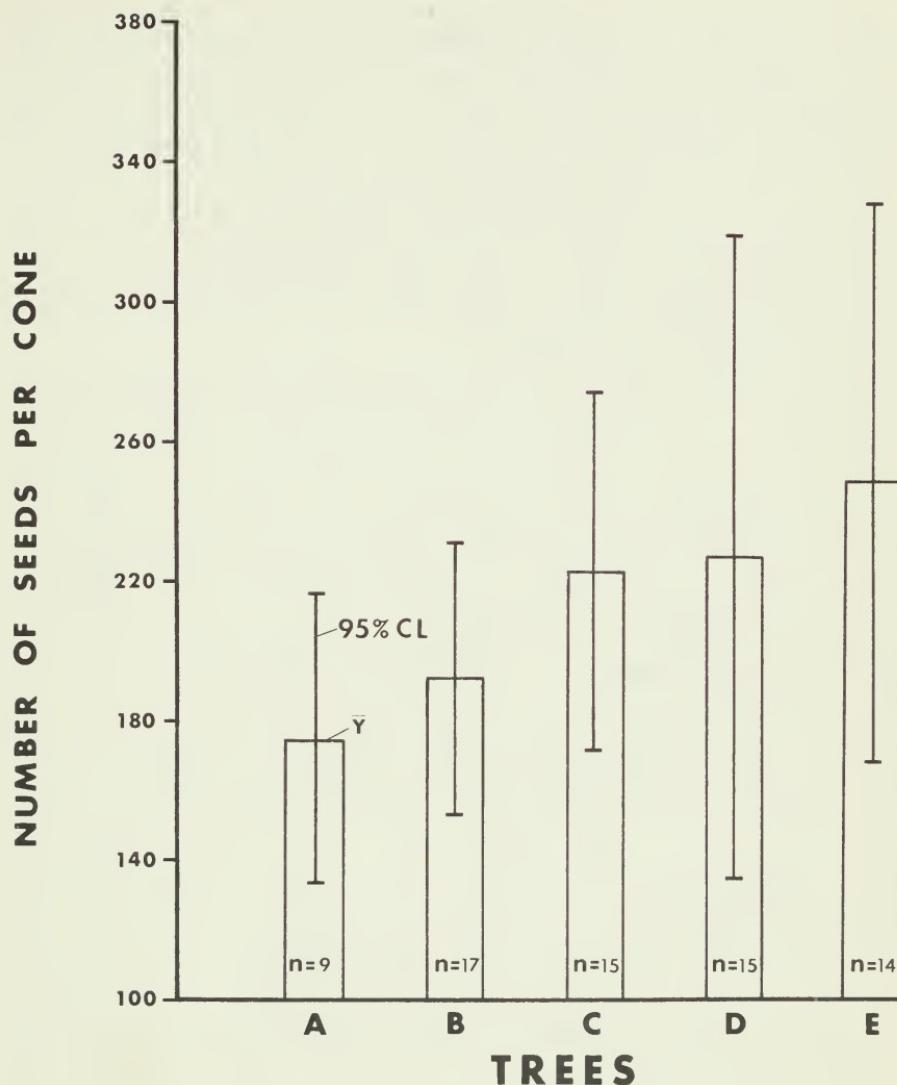


Fig. 38. Variation in number of seeds per cone for different trees. Paired t-tests showed that AC, AE and BC differed ( $p < .001$ ) and AD and BE differed ( $p < .05$ ).

series pattern while this one has a 5/8 pattern of cone scale spirals. This ratio still fits the series.

The factors affecting seed fall are varied but generally are of two major types, namely those affecting cones in the trees so that they release seeds, and those that cause cones to fall. The work of *Phymatodes nitidus*, a cerambycid beetle, is of prime importance in the tree (see Chapter 8). In addition, the Douglas squirrel may feed upon cones in the tree and release seeds. We inferred this happened in 1966 in Trail Area when numerous

seeds were found on the ground. Finally, other miscellaneous factors may cause browning of cones in the trees, such as cone bearing branches breaking but not falling from the tree. Fires which cause or increase burn scars at the base may also contribute to the numbers of browning cones that release seeds by reducing water flow through the vascular system.

Some cones that were closed and green in the tree were observed to fall to the ground from storm damage, and thus to release seeds on the ground. Douglas squirrel cut cones often yield seeds on the ground, whether through the feeding activities of the squirrels or from having been forgotten by them (see Chapter 9).

A nine month catchment of fallen seeds and cones revealed a highly variable number from one sample plot to the next. Twenty-five plots, each  $1\text{ m}^2$ , had 983 seeds on them for a mean of 39.3 ( $SD=57.2$ ) seeds per  $\text{m}^2$  (range 0 to 182). The plot with 182 seeds also had 15 cones present. In another seedfall study of 1.5 months (Sept. & Oct. 1964), 203 seeds were collected on the  $25\text{ m}^2$  plots. When combined, these data yield a mean of 54.2 seeds per  $\text{m}^2$  per year or 542,000 seeds per ha. The same area (North Area) produced 2,419 seeds in  $28\text{ m}^2$  plots for an average of 86.4 seeds per  $\text{m}^2$ . Pooling data from both years (1964 and 1965), an annual seed fall of about 860,000 seeds per hectare is estimated. The density of the mature giant sequoias in the area is about 6 per hectare.

In tests for rodent predation on seeds, ten screened plots  $\frac{1}{4}\text{ m}^2$  collected 63 seeds, while the adjacent  $25\text{ m}^2$  plots collected 327 seeds. The  $\frac{1}{4}\text{ m}^2$  plots, if adjusted for their smaller size, would have collected approximately 252 seeds per  $25\text{ m}^2$ . Apparently predation was not effective in reducing seed numbers on the exposed  $\text{m}^2$  plots inasmuch as they had more seeds per  $\text{m}^2$  than the enclosure plots. Those seeds which come from cones on the ground probably play a small role in disseminating the species because the cones fall beneath existing trees. The seeds released in the tree tops have the potential of being carried laterally great distances. Stecker calculated that seeds fall at about 1.8 m (6 ft) per second and may be dispersed laterally as much as 502 m (1647 ft).

In a detailed ground study, we found an estimated 7520 seeds per  $\text{m}^2$  had fallen by July after a fire the previous September. Only about 1% of these seeds appeared viable in July via the snap test.

The  $2\text{ m}^2$  plots, under 11 giant sequoias that were monitored daily from August 1 through September 6, 1967, yielded numbers that varied from 2 to 9 seeds per day with an average of 2.4 seeds per  $\text{m}^2$  per day. It appears that seeds fall from trees at a fairly consistent rate during the late summer. If this rate was representative, and it is probably high because it was under a dense stand of mature sequoias, over 8 million seeds per hectare could fall per year.

Once seeds reach the ground, by whatever means, viability must be sustained until proper germination conditions are present. Seeds falling

during the summer are often exposed to desiccation and other problems on the forest floor. In a study of 1000 seeds recently removed from fresh cones and placed on the ground, the percent apparently viable in snap tests dropped from 45% on the first day of exposure to 0% on the 20th day. A parallel study of 100 seeds per test for germination in native soils revealed similar results. After one day the germination rate was 38% and after 10 days germination had dropped to only 19%.

Seeds tested for germination in petri dishes with various concentrations of the cone pigment showed a statistically significant ( $p < .01$ ) delay and reduction in germination at the two highest concentrations of 22 and 18% when compared to the other concentrations (Fig. 39). The data were statistically treated as a regression of  $y$  on  $x$  with t-tests of standard deviations of means of  $y$  (Grindeland pers. comm.).

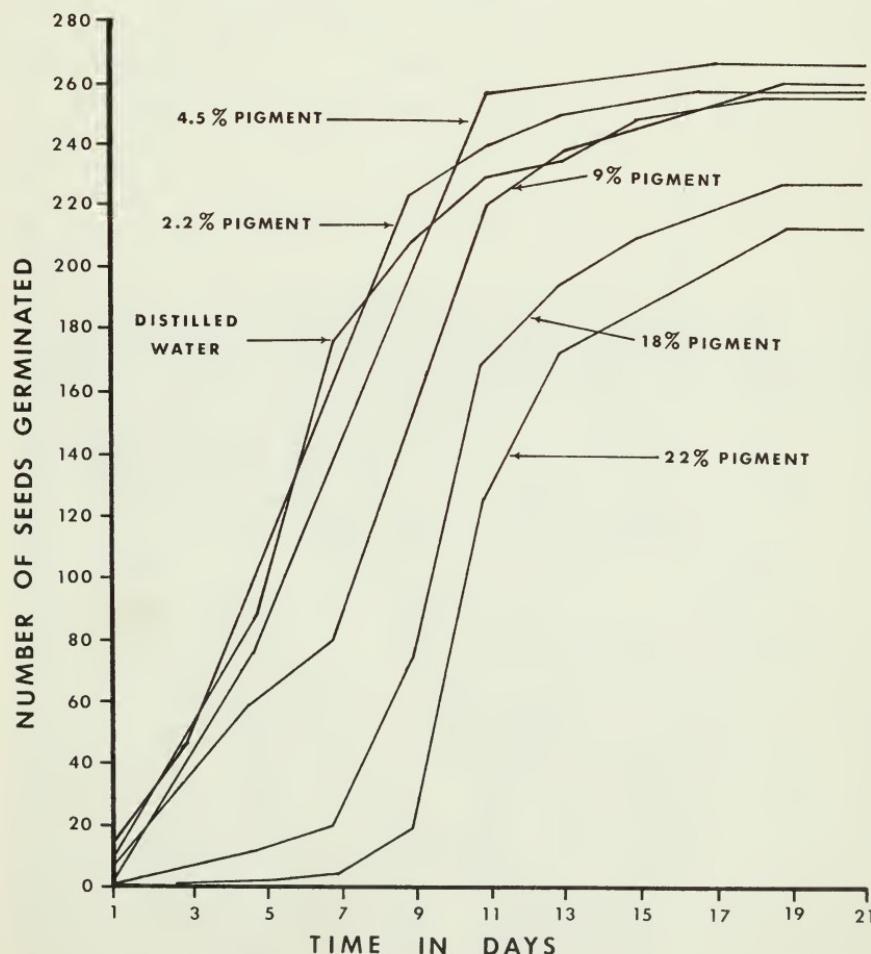


Fig. 39. Germination of giant sequoia seeds in a gradient of pigment solution concentrations and distilled water.

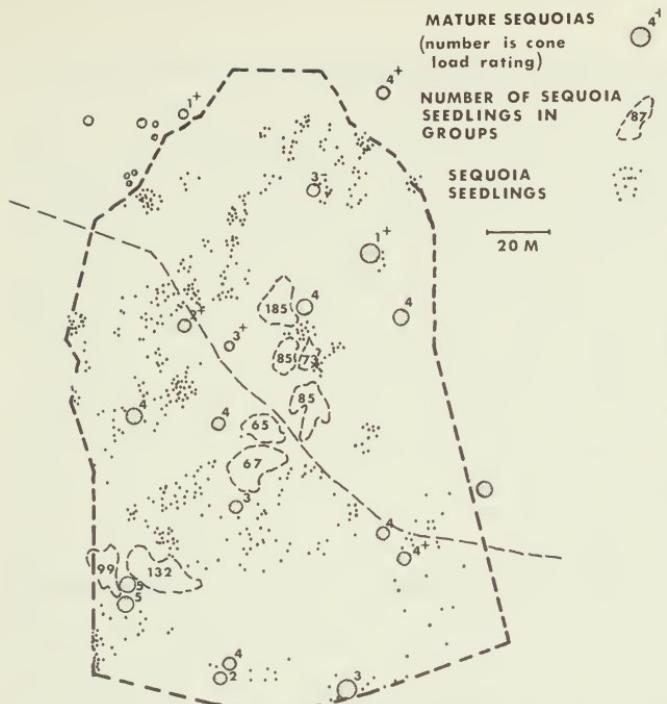
## Seedling establishment

The pattern of seedlings established in a given area was highly variable (Fig. 40). The densest patterns were southeast of mature giant sequoias, thus suggesting that the prevailing winds had been a factor (Fig. 41). Also, it seemed evident that the fires may have played a part. In one case, heat from a burn pile may have been sufficient to brown cones and thus release substantial numbers of seeds, while in another situation the fire was hot enough at the base to cause sloughing off of the bark and cambium, and may have also interrupted water transport to the cones high in the tree, drying them and releasing seeds.

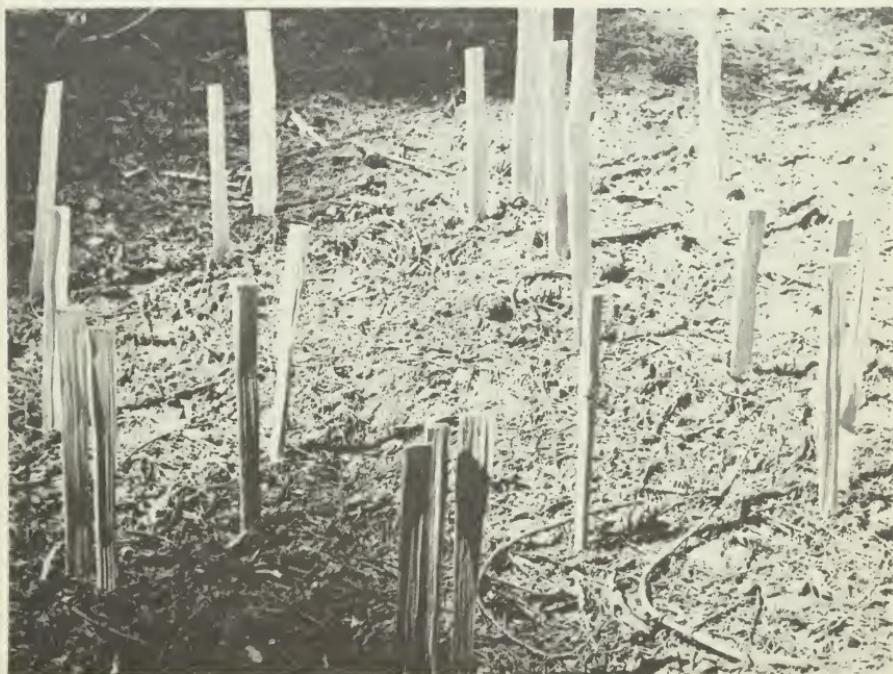
Although the first manipulation and use of fire was in September of 1964 in North Area, no seedling sequoias were observed in the treated section. Possibly, however, low seedfall and adverse environmental conditions produced this unexpected result. A bulldozed fireline in Trail Area the same year produced 30 individuals which were numbered and staked as of August 23, 1965. None of these seedlings survived until 1974.

In a survey of the presence of first year giant sequoia seedlings in control versus test sections it was apparent that the fires and manipulations had greatly encouraged establishment of giant sequoias. In the dry year of 1966, 1,565 first year seedlings were located in the Trail Area test section, while only 10 seedlings were found in the control section. Almost 30 times as many giant sequoia seedlings were present in the treated sections of the areas as in the control sections of the meter wide transect survey by Shellhammer, made during the wet year of 1969 (Table 6). The sequoia seedling population had dropped by 86% when surveyed again five weeks later in the last week in August. The treatments also seemed to be favorable to the other tree species, but to a much lesser degree as far as number of seedlings was concerned (Table 7). White fir and sugar pine seedlings showed a 5.3 and 2 times higher density, respectively, in the treated sections than in the control sections (Table 7).

It seems, therefore, that the "window" opened in the forest floor by fire to encourage the giant sequoia to become established was extended an additional year by the high precipitation. That is to say, if normal or lower than normal precipitation had occurred in 1969, the abundance of giant sequoia seedlings would probably have been very low in both treated and control sections. As a general observation, giant sequoia seedlings do come up each year on undisturbed sites, but only in exceptionally wet years are they at all numerous. We therefore infer that conditions are most favorable to giant sequoia reproduction for a period of two or three years after a disturbance to the forest floor. After that time very few seedlings manage to survive even though some seeds germinate each spring.



**Fig. 40.** Concentrations of giant sequoia seedlings adjacent to mature trees. See Chapter 9 for cone load rating.



**Fig. 41.** Dense stand of staked seedlings (in 1 m<sup>2</sup> area.)

**Table 6.** Giant sequoia seedlings per hectare (July 1969) in treated (1902m<sup>2</sup> sample) vs. control (2495m<sup>2</sup>).

Area	Years after Treatment	Treated	Control	% Control of Treated
North	5	44	0	0
Trail	4	333	31	9
Ridge	4	592	75	13
South	3	709	64	9

**Table 7.** Tree seedlings per hectare (July 1969) in treated (1902 m<sup>2</sup> sample) vs. control (2495 m<sup>2</sup>).

Area	Years after Treatment	Treated			Control		
		White Fir	Sugar Pine	Incense Cedar	White Fir	Sugar Pine	Incense Cedar
North	5	117	0	0	18	19	0
Trail	4	90	15	166	20	10	21
Ridge	4	281	112	0	37	113	0
South	3	458	137	0	129	0	0

### Seedling mortality rates

During the study years, the 7,666 live first year seedlings that had been staked in 1964–1967 decreased to only 418 live seedlings by 1974. Thus the treatments, after 10 years, have induced a density of about 90 small trees per hectare while there were none in the control areas. An additional 44 unstaked seedlings of unknown age were observed in the treated sections. These may either be ones that have somehow lost their identification stakes or were not staked at all. They may thus account for part of the loss which is discussed later under miscellaneous factors.

A population of 163 ten-year-old sequoias in Converse Basin (Fig. 3) was followed from 1964 to 1974. During that period there was only a 21.5% mortality, or 2.2% per year on the average. The population was located on three sites identified as good (in a drainage way), moderate (in a swale), and poor (near a ridge top). The sequoia seedlings on various substrates yielded a clear picture as to the importance of hot fires to seedling survival (Table 8). The survival percentage of seedlings growing where there had been a burn pile was 7.7 times greater than the percentage survival of seedlings on other substrates. The data for the 1968 South Area population are biased because the seedlings were found during the last week in August and the first week in September rather than during early summer. Selective die-off of those on other than the burn pile substrate had already occurred, therefore it is possible that a higher percent figure of survival was obtained for this population than the other three populations. If the 1968 South Area population is excluded, the seedlings on burn pile soils survived at 11.5 times those on other substrates.

Desiccation during the summer months appears to be the major factor in mortality of seedlings (Table 9). More than half (52.8%) of the seedlings discovered during the dry summer of 1966 died due to desiccation. The only other discernible factor accounting for more than 1% mortality was insect predation at 3.5%. Total mortality at the end of the summer was 62.5% for 1966 but only 26.3% for the 1967 seedlings. Inasmuch as the precipitation was only 78.1 cm (30.75 in) in the 1965–1966 season while it was 172.7 cm (68 in) in the 1966–1967 season, a drop in desiccation mortality might be expected. In contrast, the mortality due to arthropod damage increased from 1966 to 1967 (5.7% to 25.4%). The major mortality (67%) for both 1966 and 1967 seedling populations was desiccation.

Whereas the average of 39.4% mortality was observed during the three summer months of 1966 and 1967, only 25% died during the nine months of fall, winter and spring of 1967–68. The highest weekly mortality rate for the 1966 population of seedlings was 13% during the month of August. The weekly rate dropped off dramatically to only 4% by September. A population of 1378 seedlings in October of 1967 dropped to 1040 by June of 1968. The summer mortality averaged about 13% per month but mor-

**Table 8.** Percent survival of giant sequoia seedlings on burn pile substrate vs. other substrates, as of 1974.

Area—Year <sup>a</sup>	Burn Pile % (# Surv./Total)	Other Substrates % (# Surv./Total)
Trail—1966	20.0 (7/35)	2.1 (31/1452)
Trail—1967	15.6 (42/269)	1.6 (55/3372)
South—1967	31.4 (48/153)	2.3 (17/750)
South—1968	43.5 (70/161)	14.9 (121/811)
Total	27.0 (167/618)	3.5 (224/6385)

<sup>a</sup>Year, means the year the seedlings were staked and numbered.

**Table 9.** Factors involved in giant sequoia seedling mortality in Trail Area (1966 population N = 1565, 1967 population N = 3641).

Factor	Total Seedlings		Percent Mortality		1966 + 1967	
	1966	1967	Seedlings Dying	1966	1967	Those Dying
Desiccation	52.8	12.9	84.4	48.9	24.9	66.9
Arthropods	3.5	6.6	5.7	25.4	5.8	15.4
Heat Canker	0.5	2.4	0.8	8.9	1.8	4.9
Birds and Mammals	0.7	0.7	1.1	2.6	0.7	1.8
Fungi	0.4	0.2	0.6	0.6	2.3	0.6
Miscellaneous <sup>a</sup>	4.6	3.5	7.3	13.5	3.9	10.4
Total	62.5	26.3	100.0	100.0	39.4	100.0

<sup>a</sup>Miscellaneous includes those covered by debris, washed away, or not accounted for, an estimated 70% probably were covered by debris.

**Table 10.** Giant sequoia seedling survival with respect to developmental stage during summer (N= 1753).

Developmental Stage	Percent Survival
Cotyledons only	20
Cotyledons and secondary leaves	27
Secondary leaves only	34
Secondary leaves & branches	74

tality was only 3% per month for the rest of the year. These data support the contention that summer desiccation is the major mortality factor for giant sequoia seedlings.

Giant sequoia seedling survival was not only dependent on conditions of substrate and such mortality factors as insect predation, but also varied according to developmental stages (Table 10). Those seedlings which had reached only the cotyledon stage in the summer had only a 20% survival by October, while those which had developed secondary leaves and also started branching, were able to survive at about 75%. Inasmuch as seedlings grow roots proportionally larger than shoots, it seems reasonable to suggest that the larger shoots supported larger roots which may have penetrated to greater depths. They had reached the receding soil moistures which helped them survive beyond the summer months into October.

### Growth of giant sequoias.

The four populations of giant sequoia seedlings that were measured for shoot growth had an average height of only 31.8 cm in 1974 (Table 11). The shoot height of seedlings in South Area were significantly greater statistically ( $p < .001$ ) than those in Trail Area. Those growing in burn pile substrates in South Area were significantly taller statistically than those in other substrates. The mean growth per year in Trail Area was 3.2 cm, while seedlings in South Area grew at about 4.5 cm per year.

The tallest seedling in 1974 was 135 cm and was growing in a burn pile substrate in South Area. As it was only 7 years old when measured, it had grown at the rate of almost 20 cm a year. The tallest seedling in the other substrates was only 71 cm tall. The smallest seedling still alive in 1974 was only 4 cm tall and was observed in Trail Area on other than burn pile substrate. It was 10 years old, thus averaging only 0.4 cm growth per year.

**Table 11.** Average heights (cm) of giant sequoia seedling shoots on burn pile substrate versus other substrates, as of November 1974.

Area and Year	Burn Pile			Other			Calculated t values
	n	$\bar{Y}$	s	n	$\bar{Y}$	s	
Trail 1966	7	21.1	7.9	59	28.3	18.8	NS
Trail 1967	19	19.7	10.3	45	27.6	17.75	NS
South 1967	43	51.6	28.8	21	24.6	14.4	4.02 <sup>a</sup>
South 1968	74	43.0	27.5	132	25.4	14.5	6.10 <sup>a</sup>

<sup>a</sup>p<.001

Seventy first-year sequoia seedlings were measured for height at the end of summer after light determinations had been made at their sites in mid-July. The correlation coefficient for height with percent of full sunlight was positive, but only 0.34 and therefore not significant.

When seedling shoot growth for a summer was analyzed with respect to root growth and site, it was determined that seedlings produced roots 2 to 2.5 times as long in depth as shoots. The amount of growth for each segment of the plant was not significantly different when seedlings in Trail Area were compared with seedlings from the apparently drier Ridge Area. However, the proportions were 34.6% shoot growth and 65.4% root growth at Trail Area, while Ridge Area seedlings had 28.7% shoot growth and 71.3% root growth; thus roots were longer in proportion to the total length of the main axis of the plant in the drier site.

The growth of 10 to 20 year old giant sequoias was ascertained by following three populations in Converse Basin. The good site (drainage way) trees grew at the rate of 17 cm per year (Fig. 42). The moderate site (mesic slope) trees grew at about 7 cm per year. And the poor site (dry ridge) trees grew at only about 1 cm per year. The overall mean growth was only about 5 cm per year. The maximum growth rate for the 10 tallest trees on the good site was about 25 cm per year. The fastest growing sequoia on the good site grew at the rate of 56 cm (1.8 ft) per year.

The growth rate of giant sequoias older than 20 years was investigated by analyzing the data of the Evans Survey of the South Calaveras Grove in the central Sierra Nevada of California. The analysis of a Converse Basin population described earlier indicates that giant sequoias increase in diameter for the first 800 years at an average of 1 ft per 100 years. The height data suggest that from 100 years of age until 400 years the annual

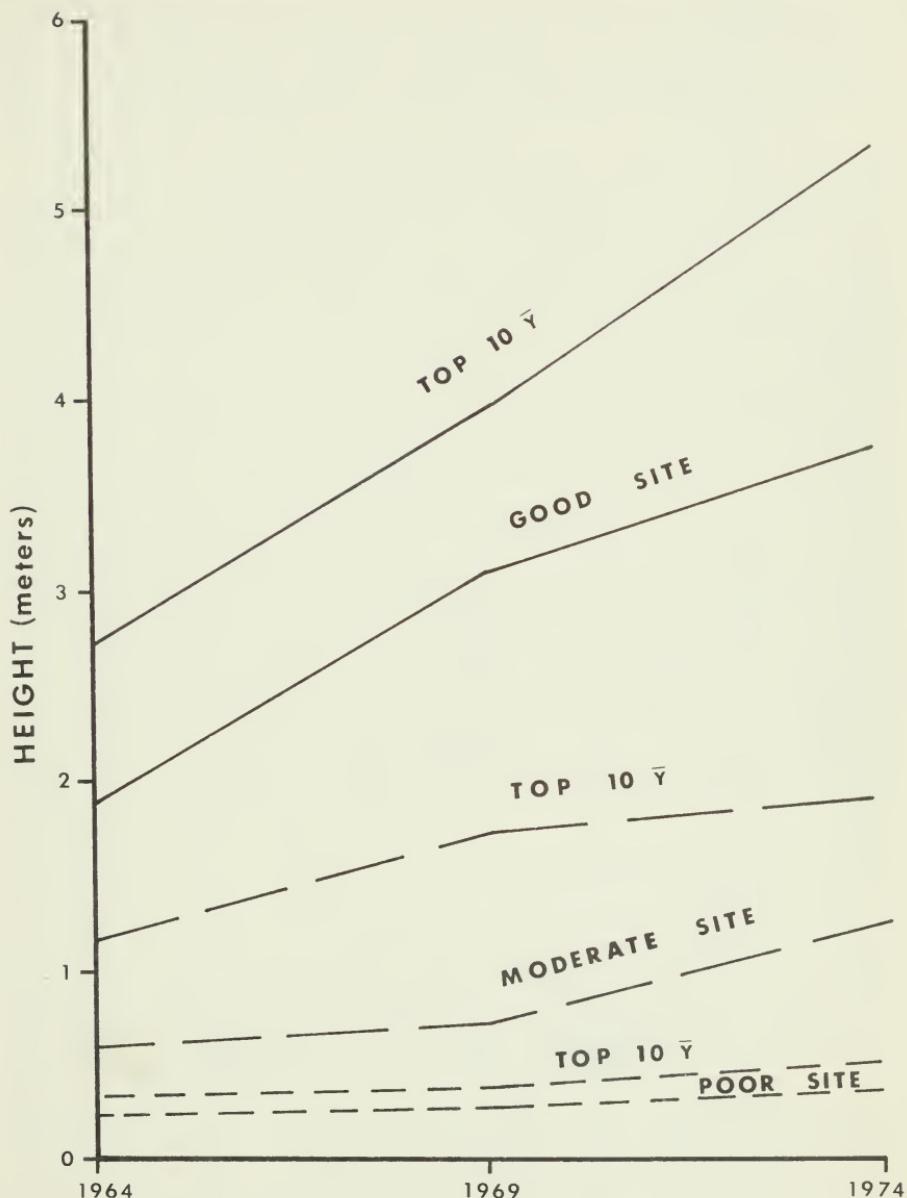


Fig. 42. Site quality and growth rate of giant sequoia saplings.

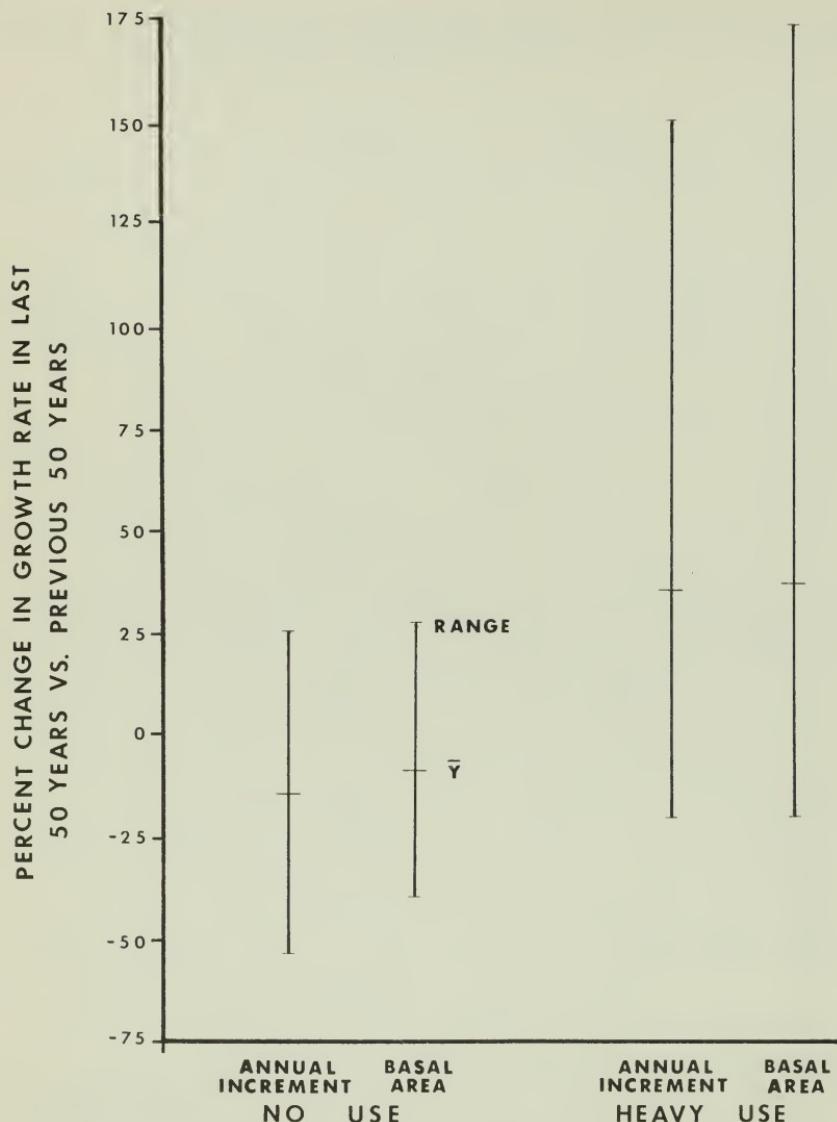


Fig. 43. Growth response of large sequoias to two levels of human activity. Mean annual increments showed significant difference,  $p < .001$ .

vertical growth rate is about 12.2 cm. After reaching 4 ft in diameter, or 400 years of age, the vertical growth rate declines and typically levels off near 76 m (250 ft) high at between 800 and 1500 years of age. The maximum height obtained by a mature giant sequoia is probably about 110 m (310 to 320 ft).

One impetus for the investigation of the effect of fire on giant sequoia regeneration was the apparent greater growth rates of trees in heavy use areas than in low use areas (Fig. 43). Highly significant differences ( $p < .001$ ) between the two areas were noted for average annual increment. The statistical test used was Wilcoxon's rank sum test (Hollander and Wolfe 1973). Those trees subject to heavy use ( $N = 20$ ) included individuals with substantial portions of their root systems covered by roads and/or buildings. Sequoias ( $N = 19$ ) far removed from such activities were cored and found to be growing at a rate not only considerably slower than those subject to heavy impact, but slightly less than growth rates fifty to one hundred years earlier. The question thus raised was, were giant sequoias growing slower in the remote areas due to the lack of natural disturbances such as fire? The experimental burns were designed to see if growth would increase in those trees subject to treatment, as well as to remove accumulated forest floor fuel, and thus induce sequoia reproduction. Five of 15 examined sequoias in 1974 had grown at a significantly faster rate ( $p < .05$ ) after the treatment in the treated sections than before treatment. The remaining 10 trees showed no significant change in growth rate. None of the 12 trees examined in the control sections showed significant change in growth rate before versus after treatment.

Grove expansion and longevity of remnants were examined in Redwood Mountain Grove, Grant Grove and Lost Grove (Fig. 3). A casual inspection of the North Calaveras Grove was also made. All of these groves have young trees over 30 m (100 ft) beyond the last large mature tree in at least one point along the perimeter. The Giant Forest inventory shows small trees to be on the periphery in several places. When cored, the young trees were determined to be about 100 years old and coincided with fire release patterns (i.e. dramatic increased growth) in the nearest large giant sequoias in Lost Grove and Redwood Mountain Grove.

The length of time that fallen sequoias have been down in a moist habitat was investigated by coring 6 trees of various species growing in the root pits of sequoias that had fallen into meadows. The trees were at the edges of Crescent, Round, and Log Meadows in the Giant Forest grove in Sequoia National Park. The trees cored at Crescent and Round Meadows were giant sequoias and thus there is a high probability that they came in immediately after the large trees fell because soil conditions are optimal for sequoia regeneration for only a few years after a disturbance. The trees cored at Log Meadow were two sugar pines and three white fir. As these two species produce relatively large seeds which can tolerate thick

duff, they may have come in several years after the sequoias had fallen. However, it is most likely that they seeded in a year or so after the large trees fell and opened up a favorable substrate. The oldest tree examined growing in a sequoia root pit was an estimated 135 years of age.

## *Discussion and summary*

### *Seed production*

The giant sequoia produces seeds at a prodigious rate. Not only does it produce seeds at over three times the rate of its closest relative, the coast redwood, on a seeds-per-cone basis, but we determined that it sheds approximately 1,000,000 seeds per hectare per year. Furthermore, when hot fires burn through a giant sequoia forest, seed fall may increase to over 20,000,000 per hectare. This increased seedfall would thus occur at a propitious time when forest floor conditions were optimal for seed germination and seedling survival.

Seeds falling at times other than shortly after a fire are subject to adverse conditions, such as thick litter and duff, and quickly die or fail to produce seedlings. Minor disturbances to the surface stratum, however, enable a few seeds to germinate under satisfactory conditions. An uprooted tree or a river deposit may provide a suitable substrate. Muir (1878) contended that the falling of giant sequoias alone would provide enough suitable substrate for sequoia regeneration. However, the fact that at least a few young sequoias should then be found in almost every fallen giant sequoia root pit is not borne out by field inspection of such root pits. Young sequoias are occasionally found in large giant sequoia root pits, but they are the exception not the rule.

Although exposed mineral soil favors seedling survival in contrast to duff and litter covered surfaces, it is not necessary for seed germination. This concept that mineral soil is required for seed germination continues to persist (Schuft 1972) even though ample evidence was provided by Stark (1968b) that wet litter provides a good germination medium. In 1969 we observed several giant sequoia seedlings in litter and duff that were over 30 cm (1 ft) in depth. In nature however, this medium rapidly dries out in the summer dry period and the seedlings die (Stark 1968a). When wet, the duff may also enable pathogenic fungi to attack the seedlings.

The seeds produced in the cones are released to become potential seedlings in two major ways. There appears to be two complementary reproductive strategies that have evolved in the giant sequoia. One is the persistent constant release of seeds throughout the year and throughout the decades in the absence of fire. The other strategy is the dramatic evulsive event that fire invokes, where seeds are released in tremendous numbers. The constant rain of seeds and cones released by Douglas

squirrel and *Phymatodes nitidus* activity provides a seed inoculum which may find suitable ground conditions in the root pits of fallen trees or the action of streams and avalanches. However intermittent, fire, particularly hot fires, may provide an unusually heavy seedfall. The fires need not be intense throughout the entire area burned, but may, due to the uneven presence or absence of heavy fuel, vary greatly in temperature (Kilgore 1972). These hot spots, as was shown in our burn pile areas, induce exceptional increase in seed release and provide the most suitable seedling substrate.

An additional factor in seed germination may be the allelopathic effects of the cone pigment. Our tests indicated that the higher concentrations of the cone pigment delay and reduce germination. Inasmuch as the pigment is a mixture of organic compounds (Kritchensky and Anderson 1955), it is probable that the high temperatures of fires would destroy it. It is also water soluble and thus would fit the characteristic of other allelopathic substances which prevent germination until sufficient water dissolves and carries them away. The increased number of sequoia seedlings observed in nontreated sections in 1969 after a winter of exceptionally heavy precipitation supports this hypothesis. In addition, it corresponds with the increased survival of seedlings in burn pile soils inasmuch as the higher temperatures there could destroy the pigment. The pigment may function, therefore, to retard some germination conditions for the seeds. The low (less than one percent) germination of seeds taken from the forest floor suggests that only those seeds that escape desiccation are likely to be involved in allelopathy.

### Seedling establishment

The two strategies of continuous and intermittent seedfall due to fire have their ramifications in seedling establishment. The continuous stratagem is faced with modest substrate conditions, at best, for germination of the seeds and the survival of the seedlings, while the intermittent stratagem will confront high seed release, favorable seed germination, and exceptional seedling growth and survival. Giant sequoia seedlings in the hot burn pile soils, excluding South Area, survived at over 11 times the rate of those in disturbed or lightly burned soils. Several characteristics of previously highly heated soils may contribute to the outstanding success, survival and establishment of giant sequoia seedlings on that substrate. Highly heated soils are more wettable. The friable nature of the soil readily permits seed and root penetration. The latter is apparently critical for survival of sequoia seedlings because summer drought appears to be the most critical factor in their mortality. Although nutrient levels may be down after a hot fire, St. John and Rundel (1976) have found that seedlings with subadequate nitrogen had a greater root to shoot ratio than

those with adequate levels. When one links the above with the shade intolerance of the giant sequoia, an interesting hypothesis emerges.

The greater the sunlight the greater the root penetration even though dry soil may be deeper in sunlit areas (Daubenmire 1974). Thus giant sequoias which survive best in sunlit areas should have greater root length in soils which are subject to rapid desiccation. Burn piles with friable soils and low nitrogen would also aid root penetration and provide the optimal site for seedling survival. Thus it is hypothesized that intermittent fires open the canopy which in turn provides greater sunlight that induces increased root penetration in the friable soil and therefore greater sequoia seedling survival and growth.

### Seedling mortality

The substrate in which the test seedlings grew greatly affected their mortality. The relatively high survival of seedlings on burn pile soils was extremely significant. Overall the data indicated a 7.7 times greater survival for those on the soil subject to the hottest fires. In fact, if the South Area data were eliminated on the grounds of the bias due to the late summer finding of seedlings, the difference was 11.1-fold. The mortality factors of the sites helped focus on the unique attributes of highly heated soils.

Desiccation was the most important among all of the factors causing mortality in the summer when mortality rates were at their highest. Apparently when seasonal precipitation was increased the mortality owing to desiccation dropped, while that due to insect predation increased to as much as 25%. An increase in mortality due to fallen branches was noted after a winter of increased precipitation. Of minor importance were heat canker, bird and mammal predation and fungal attacks.

### Growth of giant sequoias

Seedling giant sequoias grow at a highly variable rate under natural conditions. The measured extremes were 20 cm and 0.4 cm per year. The substrate, with respect to fire, appears to make a significant difference. In the extreme, seedlings on burn pile substrates grew at over twice the rate of those on substrates only mechanically disturbed. This suggests that not only was seed germination and seedling survival best on burn pile soils, but also that either root penetration and/or nutrient levels over a few years were improved by hot fires, even though their nutrients may be low immediately after a fire (St. John and Rundel 1976).

Radial growth was observed to increase in some giant sequoias which were subjected to treatment by fire and manipulation around them. Since not all of them showed a significant increase in average annual increment the question of determining past frequency of fires on analyses of deviation

in radial growth is not conclusive. However, none of the trees in the control areas (and thus not subject to fire) showed a statistically significant increase in radial growth after the dates of fires in their manipulated paired plots.

Radial growth of mature giant sequoias growing where their root surfaces were either covered by buildings or roads showed significantly greater rate of growth when compared to those not subject to such circumstances. The factors which may account for this apparent contradiction rest mainly on the apparently better soil moisture regime produced by roads and buildings. In a similar situation in the Mariposa Grove, Hertesveldt (1964) has suggested that removal of competing vegetation and reduction in evaporation may be major factors. Increased warming of the soil beneath roadways may also facilitate water uptake.

### Grove expansion

Although giant sequoia grove perimeters may be relatively stable, as suggested by Rundel (1972a), there is evidence of some expansion. Analyses of tree surveys of Giant Forest and Redwood Mountain Grove indicate that almost all large fallen trees are within the grove perimeters, but several young trees are beyond the large mature trees. Coring of some of the young trees showed that their ages were about 100 years and correlated positively with fire-released growth in the closest large giant sequoias. One young tree was 89 m (275 ft) beyond the large mature sequoias.

### Fire adaptations of giant sequoia

Many plant species exhibit adaptations to fire. Chaparral plants have seeds that germinate best when heated and have latent buds that may develop after fire. The giant sequoia also possess several characteristics that are considered as fire adaptations.

Five major criteria of fire adaptation are listed by Daubenmire (1974). Of the five criteria, the giant sequoia clearly qualifies on four of them, and to a lesser extent on the fifth. Specifically and briefly the criteria are: rapid growth, fire resistance, elevated canopies and evanescent lower branches, latent buds and serotinous cones. Rapid growth is generally acknowledged to occur in the giant sequoia, and we have recorded vertical growth approaching 60 cm (2 ft) per year in 10 to 15 year old sequoias under natural conditions. Fire resistance is apparent in the thick bark which lacks pitch and burns poorly. The bark flutes are often 30 cm (1 ft) or more in thickness near the base of the tree, and one we have measured was almost 80 cm (2.5 ft) in thickness. Seventy year old sequoias amid white firs of the same age survived the intense McGee burn of 1955, while most of the white firs died.

Giant sequoias are known for their shade intolerance and for the evanescent nature of their lower branches. These characteristics lead to an elevated canopy which in turn reduces the chance of crown fires and death of the trees even though lower branches may be killed by a fire.

Although giant sequoias apparently lack latent buds at the base of the trunk or on the roots, they are capable of sending out branches from the bole of the tree when the old branches are lost. We have observed this on trees of all ages starting with trees only a few years old. This is the one criterion that is not met to the extent of other fire adapted species such as those of the chaparral, where latent buds exist in the root crown.

Finally, the giant sequoia produces serotinous cones which may serve a dual purpose as an adaptation to rodent predation and fire. This concept will be developed further in Chapter 10.

# Arthropods Associated with the Giant Sequoia

Ronald E. Stecker

## Introduction

Relatively little scientific study had been made on the arthropods associated with the giant sequoia prior to this study. Only 20 insect species had been identified in association with this tree, and there was virtually no specific information available to suggest the total arthropod fauna or its effect upon this immense and ancient host. The first reference to insects associated with giant sequoia was by Hopkins (1903) who listed six species. The most authoritative publication on the giant sequoia of this early period with some mention of insects was that by Judge Walter Fry, U.S. Commissioner of Sequoia National Park, and Colonel John White, Park Superintendent (Fry and White 1930). Person (1933) briefly discussed two new insects associated with the giant sequoia. Keen (1938 rev. 1952) mentioned four insects in his original publication (and eight in the revised). *Phymatodes nitidus*, a central figure in this study, was reported in that publication to be a bark boring beetle.

DeLeon (1952) presented the most recent and complete review of sequoia insects. His paper is important as it named 20 insects which may use giant sequoias to complete some aspect of their life cycle. He also suggested the possible association of *Phymatodes nitidus* with the cones of giant sequoia. The preceding reports make up the limited entomological references to giant sequoia prior to 1966. This and the following chapter are a result of nearly 10 years of studies attempting to expand the body of knowledge concerning the arthropod fauna of the giant sequoia. Chapter 7 is concerned only with those insects that affect reproduction of giant sequoias.

Detailed investigations of the invertebrates of downed trees, seedlings, and living trees with foliage accessible from the ground were initiated in 1966 following observation by Hartesveldt and Harvey (Hartesveldt et al. 1975) that 3.5% of the seedlings in their study plots were being killed by chewing insects. In the summer of 1967 the research was moved from the ground into the tops of mature living trees in order to further determine the biotic interrelationships between the arthropods and the giant sequoia. Trees that were free-climbed were studied from 1967 to 1974 in Redwood Mountain Grove, Whitaker's Forest, Converse Basin, Mt. Home State

Forest, and many other locations in Sequoia and Kings Canyon National Parks. An elevator was rigged for investigation of arthropod life in the tops of two mature trees (Fig. 44), hereafter called the Albina Tree (studied in 1967) and the Castro Tree (studied in 1968-74).

The objectives of this part of the study were to answer several questions. What are the arthropods hosted by this tree? What ecological role do they play with the host? Are any species host-specific to the giant sequoia?

Most of the investigations discussed in this chapter were carried out in Redwood Canyon (Ridge, North, Trail, and South Study Areas), Redwood Mountain (NPS environmental burn zone) and Whitaker's Forest, a University of California/NPS field research station (Fig. 4). Some sampling was conducted in the Converse Basin and Mountain Home groves outside of Kings Canyon National Park. The four major objects of this study were: 1) seedling insects, 2) arthropods of downed trees, 3) those of free-climbed trees, and 4) those of elevator-rigged trees.

## Methods

### Seedling studies

Most of the insects found on seedlings had effects on seedling reproduction (see Chapter 7), hence only the aphid study will be reported here.

Forty-one seedling plots used in the study were seeded artificially or by natural seedfall. All of the plots were established in Redwood Canyon or on Redwood Mountain. Three plots (3 m × 3 m) were used in the summer of 1968; 10 plots in 1969 and 28 plots in 1970, all of uneven size and naturally seeded after fires. These plots, described in detail in Chapter 7, were studied primarily for insect activity and only secondarily as to seedling survival. Two geometrids, a gryllacridid and an aphid were investigated. The aphids were observed with a 10 power hand lens at eye-level to the ground. Paper rings 62 mm across, coated with "stickum," were placed around the bases of seedlings, but were unsuccessful when defoliators crawled through the central hole and escaped the adhesive trap. Frass collected on the discs, however, aided in determining identifications and frequency of defoliators.

### Studies of downed trees

Arthropods were collected from sequoias that had been down from 1 to 15 years or more. Specimens were cut out from under bark and xylem by axe and steel bar. Whenever possible, limbs and pieces of the bole were retained for rearing studies of the immature insects for positive identification of adults and for parasite and predator studies. They were housed in sealed cardboard boxes which had small jars as collecting windows or traps. Metal 18.9 liter (5 gal) cans were first tried, but presented

mold problems and were discontinued. Some late instar larvae and pupae were kept in rearing vials of 12.7 cm (5 in) test tubes to obtain adults.

### Free-climbed tree studies

Studies reported in this section involved approximately 30 trees from pole-size to over 60 m (200 ft), entered from the ground with little or no rope work. Most of these sequoias were in Redwood Canyon, Whitaker's Forest, Converse Basin, and Mountain Home State Forest south of Sequoia National Park. These trees ranged from 15 to approximately 200 years old and were all spire-topped. Access to several trees required establishing a prussik rope over the first sound limb at about 7.5 m (25 ft). Climbing without ropes was routine after one reached a point in the tree where the limbs were usually a meter or less apart, gradually becoming closer towards the top. Standardized numbers of sweep samples were made of the foliage with a sweep net. Sweeps consisted of sampling three linear feet of foliage using a 7 cm (18 in) net, a technique which proved most helpful in counts of Homoptera and Hemiptera. All larval forms secured from the sweeps were housed in paper and plastic bags for rearing to the adult stage in hopes of finding parasites. Hundreds of cones were secured from several dozen trees for paper bag rearing of insects and dissection of cones.

### Rigging of elevator in study trees

Access into the crown of mature giant sequoias is made difficult by the immense butt swell, the large near-ground diameter (15–27 ft) and the great distance from the ground to the first limbs, from about 27 m to 46 m (90 to 150 ft). Entry into the tops of living giant sequoias was accomplished with the help of Charles Castro of the National Park Service. Castro, utilizing climbing techniques which he developed to suppress lightning caused fires in the crowns of large trees, rigged two giant sequoias (called the Albina and Castro trees in this study). This was accomplished by climbing large fir or pine trees adjacent to (within 23 m [75 ft]) the selected study trees. The smaller tree was scaled using 8.9 cm (3½ inch) tree gaffs or timber spikes, climbing belt and circumference ropes. The latter were dual 1.9 cm (¾ inch) manila ropes permanently secured to a right "D" ring attached to a "Bashling 60 FH" climbing belt. They were used around the tree and were secured to the left "D" ring by means of a "Tenzalok" rope-lock device. One rope was used at a time to bypass branches. This technique was used to take the climber to between 46 m and 61 m (150 to 200 ft) in the smaller access tree to a point 15 m to 24 m (50 to 80 ft) above a major limb of the sequoia. Limbs facing the sequoia were removed from the access tree up to the point of attachment of a pendulum line which passed around the bole and over several limbs at

the upper most point scaled in the access tree. This line was 1.3 cm (½ in), four-strand manila tree surgeon's climbing rope, 46 m to 91 m long (150 to 300 ft). The climber then exchanged belt and spurs for a "Buckingham" tree saddle which allowed the climber to arc on a prusik dropline until he secured a hand hold on the end of a major sequoia limb (usually 40+ meters from ground level). After releasing the rope from the access tree he climbed to the 76 m (250 ft) level of the sequoia by prusik rope. An electric elevator (Albina Hi-Climber) terminal attachment was secured for easy daily access.

The rigging was modified when using the same tree two or more years in a row. Old ropes were left in the Castro Tree at the 43, 64, 73, and 85 m (140, 210, 240, and 280 ft) levels with the lowest rope reaching the ground. The following year new climbing rope was tied to the old, pulled through to replace the old, and used as entry to the elevator attachment point, where a 1.3 cm (½ in) steel cable was wrapped around the tree, with looped ends receiving the 8.4 mm (5/16 in) cable which is attached to an elevator at rest near the base of the giant sequoia. The elevator was powered by a six h.p. gasoline-operated five K.V.A. alternator stationed on the ground. A safety bull line was provided along the path of the elevator to which occupants were attached by a short sliding rope. The elevator ascended and descended at 4.5 m (15 ft) per minute. Phyllis Stecker, wife of the writer, operated the power source as well as fed and recoiled the 76 m (250 ft) power cable to the maneuvering Hi-Climber during the operation. The Hi-Climber was fitted with a shield-shaped skid designed by Harvey (Fig. 44) to eliminate excessive wear of the tree and to prevent the rig from fouling in the limbs and minimized removal of limbs along the vertical path of the device.

The investigator could either swing pendulum-like or walk out to ends of branches by means of prusik ropes [1.27 cm (½ in), four-strand manila] 91 m (300 ft) or less in length looped basally over ends of 15 cm (6 in) of larger limbs. The longer the drop line, the easier was the task of reaching the ends of these branches—some nearly 15 m (50 ft) off center. Figure 45 illustrates this technique on one of the shorter crown branches. In 1974 the use of four-strand manila rope was discarded for a synthetic three-strand called "Silvalon." This rope is very superior because of its three-fold greater strength and ease of handling.

### Methods of sampling mature trees

Sampling sequoia foliage presents unique problems. Several techniques were adapted from existing methods of ground sampling to reliably assess insect activity in the crown of living trees. Modified malaise traps (Butler 1965) and sticky boards (Roesler 1953, modified by Wilde 1962) were used during the study of the Albina Tree in 1967, and the first year in the Castro Tree in 1968. The malaise traps were constructed of war surplus mosquito



Fig. 44. Elevator and bark protecting shield turned away from Albina Tree, June 1967.



Fig. 45. Pendulum-prusik technique used by Ron Stecker in Castro study tree, west side at 270 foot level. July 1969.

nets designed to cover cots (Fig. 46). Two-thirds of one side were removed to allow insects access to the sloping, inner retainer wall. Negative geotropic response led insects up the slight incline of the inner roof of the net and through a cardboard funnel into a large plastic collection bag. Loose, fluffed paper tissue was included in the bag to take up any moisture that developed on the walls of the bag, and to keep insects from damaging each other by abrasion. Guy lines were somewhat difficult to position because of the moving branches, but the major problem was the predation upon captured insects by spiders within the plastic collection bags. Cyanide and other killing agents were tried to control the spiders but the best results came from servicing the traps once or twice a day. Malaise traps were placed at 15 m (50 ft) intervals within the 30 m to 88 m (100 to 290 ft) level of the two trees. Material secured from these traps did not necessarily come from the sequoia host but provided a starting point for insect study by gross collecting of fauna within the sphere of the tree. In addition, 60, 3 cm ( $\frac{1}{4}$  in) thick adhesive boards, of  $929 \text{ cm}^2$  (1 ft $^2$ ) of yellow surface per side were coated with a film of "Stickum Special," a commercial preparation for mechanical insect control. Boards, with 1.6 mm to 2.2



Fig. 46. Malaise trap modified for use in tree, 275 foot level of Castro Tree. July 1968.

mm (1/16 to 1/8 in) of coating, were placed at all elevations and on all sides of the tree. They were further assorted and oriented as to north-south or east-west facing alignment, and horizontal versus vertical aspect within each of these subareas of the tree. The sticky boards were very successful in that they provided greater information as to kind and general location of insects within the tree. Relative numbers through time were also established by their use.

The most important method of locating and studying exposed insects was by direct observation. The investigator could move within any portion of the tree, using drop lines, and carefully observe the activity and behavior of insects in the tree's branches.

Over 10,000 insects were collected during these investigations. They were mounted and labeled in the field by Phyllis Stecker and are housed in the Museum of Entomology, San Jose State University, San Jose, California. A reference collection of insects of the giant sequoia (and of the general area) is maintained there. Identification of these insects has been by the author and by recognized authorities of the various insect groups whenever possible. These arthropods were then analyzed as to their ecological and physical relationship within their host.

## Results

One hundred forty-three species of insects and seventeen species of other arthropods were identified as using the giant sequoia as a host (food or substrate) during some portion of their life cycle (see Appendix II for listing). Information secured from the study of the arthropods found on seedlings, downed trees and living sequoias is discussed within an ecological framework in this section.

Malaise traps and sticky boards provided broad leads as to some of the insect fauna of the standing trees. Insects caught on sticky boards were hard to clean, even with xylene solvent, while a different problem, that of spider predation, was encountered with the malaise traps. These techniques were discontinued by the end of the second year in favor of sweeping and concentrated observation of the tree canopy.

In general, the abundance of flying insects was associated with that portion of the canopy in full sunlight, or east to west sectors from sunrise until sunset. A vertical arrangement of insects in such a tall tree was suspected, but it was soon obvious that this was not the case.

### Insects of seedlings

Very few insects were found to be associated with seedlings three years of age and less. Two geometrids and a gryllacridid were found and are discussed in Chapter 7 as insects related to reproduction of giant sequoia. In 1970 an aphid, *Masonaphis morrisoni*, was common on first year seedlings (Fig. 47). Forty-four percent of the seedlings from 28 plots (numbered 14–41) ranging in size from 18 to 72 mm had aphid activity averaging 1.6 aphids per seedling of those with aphids (plots 1–13 from 1969 were not studied for aphids). This was the first record of the male morph of this species, thus only four species of insects are known to use the seedling stage of giant sequoia.

### Insects of downed trees

Arthropods were studied on trees down from several weeks to over 20 years. *Callidium sequoiarum*, a cerambycid beetle known only from this host (DeLeon 1952), was commonly found in fresh down limbs with *Semanotus ligneus amplus* (Cerambycidae) (DeLeon 1952). Both beetles mine as larval stages beneath bark less than 2 cm thick. The latter was also associated with a rodent-killed, pole-size sequoia in the Cherry Gap Grove of Sequoia National Forest in 1966 (Shellhammer et al. 1970). *Temnochila virescens* (Ostomatidae) and *Cucujus clavipes* (Cucujidae) were predatory as adults and larvae on the two cerambycids. A small, 6 mm long, cricket commonly called the west coast ant cricket, *Myrmecophila oregonensis* (Gryllidae), was found under moist bark in association with the cucujid pupal chambers. The ant cricket usually



Fig. 47. *Masonaphis morrisoni* feeding on a 52 mm seedling, in plot number 29, Redwood Mountain, 1970.

lives in a commensal state with various species of ants. An ambrosia beetle, *Gnathotrichus sulcatus* (Scolytidae), was recorded by DeLeon (1952) from trunk sapwood. It was commonly found there in the present study as well as in limbs of recently downed giant sequoia sapwood. Larvae and fresh adults of *Sirex areolatus*, a horntail (Siricidae), were retrieved from mines over one decimeter deep in heartwood of a tree which had been down for nine months.

More insects were associated with sequoias that were down for over one year than in those down less than one year (see Appendix II for complete listing). Among those found over one year were: *Trachykele opulenta* (Buprestidae) which as larvae mine 10 cm into the xylem forming horizontal pupal chambers, and stag beetles, *Ceruchus punctatus* (Lucanidae). The former beetle can kill trees undercut by streams or otherwise mechanically damaged or suppressed.

*Rhysodes hamatus* (Rhysodidae), or wrinkled bark beetles, which normally use beech, ash, elm, and other deciduous trees, and at times pines (Arnett 1960), for a host, were discovered under the bark of sequoias (which aids in further establishing this small beetle's relationship with coniferous hosts). Several wood-boring, but not wood-feeding, Hymenoptera were noted in downed sequoias. Carpenter ants, *Camponotus minor* (Formicidae) were commonly noted in stumps and in portions of logs at ground contact. Carpenter bee, *Xylocopa californica* (Xylocopidae), damage to downed sequoia was noted but no individuals were actually found. Drywood termites, *Zootermopsis navadensis* (Kalotermitidae), were also found feeding on downed sapwood and larger dried-out limb joints.

Two neuropterous predators were noted in larval mines and under bark. *Agulla assimilis* (Raphidiidae), a snakefly, was the most common. The snakefly larvae were also found in the old emergence holes. *Chrysopa carnea* (Chrysopidae), or green lacewings, were collected as larvae beneath the bark of downed trees. This insect is normally an aphid feeder ("aphid lion") and was thought to be feeding on small invertebrates or, quite possibly, using the location as a pupation site.

*Anoplodera valida*, a long-horned wood-boring beetle (Cerambycidae), was secured in the larval stage mining a 30 m (100 ft) downed sequoia in Whitaker's Forest.

The following beetles were found under the bark of downed sequoias: *Nyctoperis carinata* and *Uloma longula* (Tenebrionidae), scavengers under bark; and *Trigonurus* sp. (Staphalinidae), predators under bark and numerous in brown cones on the ground from Trail Area. *Lycidota californica* (Lampyridae) was a predator under bark, and *Ptinus agnatus* (Ptinidae) was found under loose bark and reared from small dead limbs of mature sequoias.

One of the more common insects found in sequoias down for 10 to 20

years or more was *Melasis rufipennis* (Melasidae). These small beetles were noted in densities up to 90/dm<sup>2</sup> mining old sapwood. Their old emergence holes indicated activity in past years.

### Insects of standing live trees

The arthropod fauna of living giant sequoias, unstudied before this project, offered the greatest wealth of new information. Insects with sucking mouth parts were especially numerous. Eleven out of a total of 74 insects found in the canopy of living trees had this type of feeding style. Insects that attack one to three year old giant sequoias are discussed in Chapter 7.

The following insects were among those found associated with sequoias between 3 and 25 years of age. Two plant bugs (Miridae), *Lygus hesperus* and an unidentified form, were commonly observed feeding on new foliage. *Dichelonyx vicina* (Scarabaeidae) actively fed upon sequoia foliage of this age group, as did *Sitona californicus* and *Apion* sp. (both Curculionidae). The weevils were not observed in mature trees. *Scobicia declivis* (Bostriichidae) and *Anthaxia aneogaster* (Buprestidae) were secured by sweeping the foliage of this age class. DeLeon (1952) records the latter from recently broken limbs infested with *Callidium sequoiarum*. Large leaf beetles, *Glyptoscelis juniperi xanthocoma* (Chrysomelidae), were observed feeding and were swept from foliage of sequoias at most study sites.

Sequoias 25 years and older, including the over 1,000 year old Castro and Albina elevator-rigged study trees, yielded the following insects. Five species of leafhoppers (Cicadellidae) were discovered actively feeding on new terminal foliage. The most common were *Balclutha medius*, *Idiocerus musteus* and *I. apache*, while *I. amoenus* and *I. nervatus* were found in smaller numbers. Three treehoppers (Membracidae) were secured by adhesive board traps in 1967 and were confirmed as feeding on new foliage throughout the tree from 1968 to 1970. The species were *Crystolobus nitidus* Van Dyke, *Micruitalis occidentalis* and *Platycotis minax*. Adult snakeflies (Raphidiidae), *Agulla assimilis*, were observed feeding on *B. medius*. A small psyllid, *Psylla brevistigmata* (Psyllidae), was secured throughout the study trees by sweeping foliage.

Other fluid-feeding insects included *Ischnorrhynchus resedae* (see Chapter 8) which fed as adults on new tissue in the upper one-third of the older trees, and *Neides muticus* (Berytidae-Neididae), a stilt bug, commonly found both in young and old trees. Three very small sized (1 mm) psocids, or bark lice, were found under loose pieces of bark, one species at the 60 m (200 ft) level, a second species throughout the top half of the tree, and a third species was found only in the top three meters of the elevator study trees. These insects are scavengers in the food chain. Another small (1 to 2 mm) insect, a species of thrips, was found only in

the very top of study trees and was frequently encountered while sweeping crown foliage.

*Phloeosinus punctatus* (Scolytidae), known in previous literature on giant sequoia as *P. rubicundulus*, was known only from this host, and as attacking only downed limbs (DeLeon 1952). Wood (1971) considered *rubicundulus* a synonym of *punctatus*. Dead limbs in the Castro Tree at 74 meters (243 ft) to 82 meters (270 ft) had emergence holes of this bark beetle. Adults were also collected during July in traps and by sweeping foliage.

Springtails, *Entomobria* sp. (Entomobryidae), were common in fissures in the bark throughout entire mature trees. Up to 22 individuals per brown cone were recorded at the 82 m (278 ft) level of the Castro Tree in 1967. These small, 2 mm long insects are scavengers.

*Trachykele opulenta* was found in the top 6 m (20 ft) of an 18 m (60 ft) giant sequoia near Redwood Saddle (at Barton's Post Camp). These beetles were responsible for the dieback of the terminal to this point. Emergence holes of this species were common in bark that was at least 10 cm (4 in) thick on more mature trees. DeLeon (1952) states that this species can complete its growth stages entirely within the bark. Many observations during this study agree with that statement.

Several important predators and parasites were found during the study. *Enoclerus shaefferi*, *E. lecontei* and *Cymatodera sobara* (all Cleridae) were first observed searching smaller limbs in the upper foliated portion of the Albina Tree in 1967. Their predaceous larvae were later found associated with *Phymatodes nitidus* in cones and small limbs. A lady beetle, *Olla abdominalis* (Coccinellidae), was first found in the Albina Tree and later observed in the Castro Tree feeding upon the sequoia aphid, *Masonaphis morrisoni*. A small predaceous beetle, *Nemozoma fissiceps* (Ostomatidae), was recorded in small numbers from 12 to 50 mm ( $\frac{1}{2}$  to 2 in) diameter limbs that had fallen from a mature sequoia in North Area.

Larval stages of *Syrphus* sp. (Syrphidae) were observed actively feeding upon the sequoia aphid, *Masonaphis*, the latter of which was estimated to exceed over 100,000 individuals per tree (up to 10 or more per 25 mm [1 in] of new growth). The search and seizure rate of these blind predaceous maggots was one aphid in three minutes. They were noted feeding as late as 1:00 a.m. in the Castro Tree. Adult *Syrphus* expressed territorial behavior along the margins of foliage of the study trees. *Syrphus* was preyed upon by a robber fly, *Neoitamus affinis*, that waited in ambush and would capture *Syrphus* in flight. *Syrphus* was also parasitized in the larval stage by ichneumonid and braconid wasps.

Bee flies, *Villa alternata* (Bombyliidae), practiced the same territorial flight behavior as *Syrphus*. As many as one hundred adults were estimated to be flying about the crown of the Castro Tree during the day. The larvae of these flies are parasitic in the immature stages of Lepidoptera, Co-

leoptera and Hymenoptera. However, none were reared from these hosts during the study.

Large flesh flies, *Sarcophaga* sp. (Sarcophagidae), were observed very commonly sunning themselves on the larger limbs of the trees studied.

A leaf mining fly, *Minettia flaveola* (Lauzaniidae), was extremely numerous in sweep samples of foliage, at times making up to 35% of the sample. No relationship between this fly and a host was established.

Carpenter ants, *Camponotus minor* (Formicidae), were well established in the base of the Castro Tree, being very active at night, with limited activity the first 90 minutes after sunrise. Little attention was placed in this study on the carpenter ant, which was at time of our investigations being extensively studied by the University of California team of Drs. David Wood and Charles David. Their investigations are concerned with possible buildup of this ant in fire suppression and high park visitor areas, and the ecological role of this ant in the sequoia forest (Kilgore pers. comm.). Another ant, *Leptothora muscorum*, was very active on the surface of the bark during the daylight hours between 21 m (70 ft) and 80 m (265 ft) level. There are no arboreal ants known to the Sierra prior to this observation (Pitman pers. comm.).

## Discussion

The insect fauna of the giant sequoia is small when compared to that of other conifers of the same region. It differs considerably from that treated by Southwood (1961) in the hypothesis that insect species associated with a tree are a reflection of the cumulative abundance of that tree throughout recent geological history. Insect faunas of historically newer trees are considerably larger than those of the much older giant sequoia. The insect faunas of pines and firs are usually two to three times greater than the presently known fauna from the giant sequoia.

The physical size of most of the individual insects associated with sequoia is also small. Most insects associated with adjacent conifers are likely to be twice the physical dimensions of those of the giant sequoia. There is also a preponderance of foliage-colored insects within this fauna, making them all the more indistinguishable.

In general, fluid-feeding insects with sucking mouth parts were concentrated in the lower half of the foliated portion of the trees studied, while those with chewing mouth parts were found throughout the trees with concentration in the upper third. This may be explained by water stress problems in the tops of mature trees (Tobiessen et al. 1970), where less fluid means less pitch and resins (Graham 1952), which may allow chewing (boring) insects freedom from "pitch-out". At the same time, good fluid availability such as is the case in the lower limbs, might possibly explain the greater density of fluid feeding aphids and other homopterous

insects in the bottom half of the study trees. It is the fluid pressure within the vascular tissue that forces carbohydrate-laden fluid into these insects (Chapman 1969). They do not really work for their meals.

Tobiessen et al. (1970) measured the xylem pressure potential in the Castro Tree every 15 meters along this tree's height with a pressure bomb. The measured gradient was about -0.8 bar per 10 meters height, or less than the hydrostatic gradient. Maximum water stress at the top of this sequoia approached -20 bars, which may explain the abundance of fluid feeding insects in the lower portion of the study trees.

Of the 143 species of insects encountered in this study, 4 species were found on seedlings (3 of these were also in older trees). Thirty-two insects were found in different stages of downed and dead limbs of standing giant sequoias, while 3 of these were also observed in standing dead wood of the living host. One hundred and fourteen insect species were found only in the canopy of the living tree.

The small fauna of the giant sequoia also has a small interaction, i.e. food webs. The majority of the insects are small and pigmented similar to the sequoia bark or foliage and display very little interspecific activity such as shown in the food web of *Masonaphis* and *Syrphus*—ichneumonid and braconid parasites—*Neoitamus* and *Villa*.

In summary, the giant sequoia, the largest living organism past or present, and one of the oldest, is unusual in having relatively small insects comprising a relatively small insect fauna.

# The Role of Insects in Giant Sequoia Reproduction

Ronald E. Stecker

## Introduction

The sole reference to insects affecting giant sequoia reproduction prior to this study was a brief notation by Fry and White (1930) stating that cutworms damaged plantation stock. The present study, however, revealed as early as 1966 that several arthropods, especially insects, have an impact upon the reproduction of the giant sequoia. The discovery in 1968 of the cone activity of a small cerambycid beetle, *Phymatodes nitidus*, led to studies showing the importance of this insect in the release of seeds from giant sequoia cones (Stecker 1973).

The objectives of this part of the investigation were twofold. The first objective was to measure insect-related losses of seedling sequoias and the second was to study insect activity in ovulate cones in the crown of living trees. Data were collected in respect to the latter objective to determine the extent of damage to cones, the age classes of cones used by the cone beetle, and the effect of insects upon the dispersal of seeds and reproductive potential of the giant sequoia.

The four study areas described in Chapter 2 were used in this study, as well as special plots in or near the Redwood Mountain Grove which are described in the following section. Two mature giant sequoias were rigged with an electric elevator for in-crown investigations, the first such research to be conducted 200 to 300 feet above the ground in this tree (see Chapter 6).

## Methods

A census was made of hypocotyl loss, defoliation, and damage from sucking insects of seedlings in the study plots and along several arbitrarily selected transects. The major emphasis of this study was given to measurement of cone insect activity in the crowns of pole size to mature 93 m (300 ft) tall sequoias.

### Artificially seeded plots

Seedling beds were artificially established in Redwood Canyon and on Redwood Mountain to assess insect loss of young sequoias from germination through the first seasons growth. Three plots of 3m × 3m (10 ×

10 ft) were established in the fall of 1967 and early in the summer of 1968 in Redwood Canyon at sites of different successional stages. Ten plots were established on Redwood Mountain on 1969. Finally during the summer of 1970, 28 random, uneven-sized groups of natural seedlings were marked in the latter area. The seedlings in these plots were studied primarily for insect activity and not survival as such.

Plots for 1968 and 1969 were established upon diverse sites. In each case litter and duff were removed to expose bare mineral soil. Sixty grams of seeds (approximately 12,000 seeds) were then lightly raked into the top 3mm ( $\frac{1}{8}$  in) of soil and tamped in by foot and the end of a rake. Plot 1 was within the southeast boundary line of Trail Area (Fig. 4) adjacent to the road where no natural seeding had taken place. Trail Area had been manipulated by fire in 1965. Seeds were sown during the late fall of 1967 to minimize loss of seed viability due to desiccation. Plots 2 and 3 were located in Redwood Canyon, 0.4 kilometer ( $\frac{1}{4}$  mile) south of South Area. Duff was removed to expose mineral soil and the plots were provided with approximately 1.3 cm ( $\frac{1}{2}$  in) of water per week during the growing season by means of perforated five gallon tins and by fire-control pumper truck. Plot 2 was a shaded depression surrounded by white fir.

Seeds were planted the last week of November 1969, just before the winter snowfall, in 10 prepared seed beds measuring 3 m  $\times$  3 m (10  $\times$  10 ft). These plots were numbered from 4 to 13. Seven of them were situated within the 305 m (1000 ft) wide 1969 National Park Service environmental burn along the ridge of Redwood Mountain, which extended 1.6 kilometers (one mile) to the south from Redwood Saddle (Fig. 4). Three control plots, cleared to mineral soil, were established outside that burn.

### Naturally seeded plots

It was noted in 1970 that seedling establishment from natural seedfall of the 1969 environmental burn atop Redwood Mountain was at least four times greater than that found in the prepared seedbeds in the same area. This was surprising considering the hand seeded rate of approximately 12,000 seeds per 3 m<sup>2</sup> (10 ft<sup>2</sup>) plot. The apparent heavy natural seedling establishment was in part a result of cones that had been killed by rising masses of hot air during the environmental (fuel reduction) burn (Kilgore 1970). Seed drop was apparently from cones from the 30 to 70 m (100 to 225 ft) level of these trees. Study efforts were then concentrated on this area of naturally seeded reproduction, where seedling density reached a maximum of 82 individuals 1 dm<sup>2</sup>. Twenty-eight plots, each with 10 tagged randomly selected seedlings, were picked from within the 305 m (1000 ft) wide area. These plots were numbered from 14 to 41.

One meter wide transects were also established at Trail and South Areas to assess the loss to seedling insects during the summers of 1968 and 1969. The transects were laid out on diagonals with sampling taken one meter in every 10 meters.

### In-crown sampling methods

Techniques described in Chapter 6 were used to gain access to the cone distribution in a number of study trees (the Albina, Castro and in other free-climbed trees). Approximately 4,000 cones were removed from these trees, opened and cut in quarters. Most cones were sliced using a large Corona pruner with a 10.2 cm (4 in) blade with one of the 74 cm (30 in) handles attached by clamps vertically from a heavy, broadbased platform. The free handle provided sufficient leverage for clean cuts of both green and brown cones. Heavy knives and meat cleavers were excluded as too dangerous to use repeatedly, and because they lacked the precision of the oversize pruner. Cones were bisected lengthwise twice, providing quarters of cones for easy examination. Most quarters were observed under a binocular microscope using 15 power magnification.

A major emphasis in this study was focused on the effects of insects upon the ovulate cones of the giant sequoia. The persistence of cones in this species allowed for precise and quantitative observations on insect activity relative to location, age and spatial distribution of the cones. This necessitated a total census of the cone load in at least one tree. A mature sequoia usually contains from 10,000 to 30,000 or more cones. They are unevenly distributed in a vertical and horizontal manner. The distribution of cones in the Castro Tree was carefully established by hand counting in order to avoid the high error associated with visual methods (50% or more). The cone count and mapping was made of the entire Castro Tree in August 1970. Age classes of cones were tagged using different colors of plastic "flagging" tape for each respective year.

New cones which are pollinated during early spring are approximately one-fourth smaller than the second year cones. These "yearling cones" are light lime green and are the ones most easily observed from the ground because of their apical position. Older age class cones are usually obscured by foliage. The first year cones are also the only ones with a 2 to 4 mm aristate tip (bristle) distinctly projecting from the center of each scale's umbo (Fig. 48). This tip dries, shrivels and starts to disappear by the second year. Thus, first and second year cone classes were easily identified for census purposes.

Selected cones with known insect activity were encased in live traps of two types; one, a nylon mesh cylinder with cord ties at each end, the other, a 7.6 × 12.7 cm (3 × 5 in) cotton mailing bag with a drawstring end. Cones selected for rearing insects were housed in number eight Kraft paper bags. The bags were used even though a few beetles bored out through the paper. Cardboard boxes and large metal cans were tried, but proved unsuccessful because of the development of mold on the moist cones.



Fig. 48. First year cone which shows aristate tips of scales.

*Results*

Insects appear to play a major role in the reproduction of giant sequoias by releasing seeds from cones in standing trees and causing loss to seedlings.

### Seedling loss to insects

By August of 1968 6% (52 of 871) of the cotyledon stage seedlings in plot 1 had had their tops chewed off. Plot 2 (where 206 seedlings developed) sustained 3.4% (or 7) of the seedlings lost to chewing insects, while plot 3 sustained a 4.2% loss or 41 out of 966 seedlings to chewing insects. Deer ate 26 seedlings one night in what appeared to be four random browsing attempts in a line across plot 3. The transects in Trail and South Areas revealed 3.7% and 4.3% mortality respectively from insect activity. Fig. 1 shows severed hypocotyl loss to insect feeding, which can be easily distinguished from deer browse by the mandibulate markings.

Insects responsible for the above chewing loss were early instars of *Psistocaulophilus pacificus*, a camel cricket (Gryllacrididae), and the larva of the geometrids *Sabulodes caberata* and *Pero behresarius*. The former, an orthopteran, is a nocturnal feeder in contrast to the diurnal feeding of the caterpillars.

**Table 12.** Insect damage to giant sequoia seedlings in prepared seedbed, Redwood Mountain—1969.

Plot number <sup>a</sup>	Number of seedlings	Hypocotyl severed	Cotyledons chewed	Leaves chewed	Total % damage
4	22	6	3	5	63.6
5	12	0	1	4	41.7
6	47	8	14	6	59.6
8	15	3	1	3	46.7
9	8	0	0	2	25.0
11	28	8	2	6	57.1
12	17	1	2	2	29.4
Total	149	26	23	28	
% insect activity	51.6	17.5	15.4	18.8	

Three control plots (Nos. 7, 10, and 13) were void of seedlings.



Fig. 49. Severed hypocotyls of giant sequoia seedlings due to insect feeding.

Inspection of the prepared, hand-seeded plots numbered 4 to 13, in the early summer of 1970, revealed that 17.5% of the seedlings were completely chewed off (hypocotyl severed) (Table 12). Another 34.2% showed chewing damage to either cotyledons or needles. Control plots did not contain any seedling development.

The loss of seedlings established by natural seedfall in plots numbered 14 to 41 is summarized in Table 13 (including death by deer trampling and digging by squirrels). Table 14 shows loss in one  $0.6 \times 12$  meter ( $2 \times 40$  ft) burn trough which contained 2101 seedlings in a dense stand. Total losses to geometrids and gryllacridids was 23.7% at midsummer and in-



Fig. 50. Larva of *Phymatodes nitidus* and mining activity in a giant sequoia cone.

creased slightly to 29.2% by fall. Both percentages are for the total number of seedlings present at that date. No seedlings were observed in control plots outside of the burn area.

#### Insect activity in cones

Oviposition by *Phymatodes nitidus* usually takes place in the cone-peduncle attachment area. Larval stages usually penetrated and mined the axial shaft of the cones, reaching into individual cone scales (Fig. 50). Maximum projected linear length of mines was 21.2 cm. entering up to 15 scales. Larval frass was characterized by its fine, bicolored appearance. The particles which were tightly packed in the larval gallery resembled a coarse mixture of salt and pepper, composed of cream to white pieces mixed with amber to brown components. Frass was usually expelled in the terminal 5 to 12 mm of gallery where overwintering pupation takes place. The diameter of these mature larval mines was less than 2 mm in width. Larval mining severed the vascular connections to the individual cone scales causing drying, shrinkage and the resultant release of the seeds that were borne on each scale. The resultant drying caused the browning of cones. Larval mining, exclusive of the cone, but still causing browning, occurred in the peduncles of 7% of the cones while peduncle mining in conjunction with that of the cone occurred in 13% of the

Table 13. Random seedling study plots showing insect and other damage to natural regeneration in fuel reduction burn on Redwood Mountain—September 1970<sup>a</sup>.

No. seedlings	No. damaged severed	Hypo- cotyl. eaten	3 cotyledons eaten	2 cotyledons eaten	1 cotyledon eaten	Maj. leaf dam.	Mod. leaf dam.	Minor leaf cory. dam.	Seedlings with aphids <sup>b</sup>	Dead by deer	Dead by rodents	Dead by drought etc.
280 <sup>c</sup>	76	34	7	15	12	16	26	41	105	21	10	54
% of total <sup>d</sup>	27.1	12.1	2.5	5.4	4.3	5.7	9.3	14.6	37.5	7.5	3.6	19.3

<sup>a</sup> See appendix for complete account of each plot.

<sup>b</sup> Also counted in other categories.

<sup>c</sup> Twenty-eight plots of 10 each.

<sup>d</sup> Total above 100% because of multiple conditions of seedlings.

**Table 14.** Insect loss to unusually dense seedlings in burned log trough (2101 individuals in  $2 \times 40$  foot area) Redwood Mountain, Summer 1970.

Seedling Damage																
Portion of trough	No damage	Hypocotyl severed	3 cotyledons			2 cotyledons			1 cotyledon eaten			Major leaf damage	Moderate leaf damage	Minor leaf damage		
			July	Sept	July	Sept	July	Sept	July	Sept	July					
West quarter	208	101	69	11	18	0	17	0	18	0	19	30	13	5	53	4
West mid-quarter	398	357	34	9	11	1	16	1	18	0	14	66	2	4	49	4
East mid-quarter	330	184	4	19	2	0	7	11	2	1	26	36	0	6	22	17
East quarter	667	324	19	58	5	4	9	1	4	0	17	99	10	1	20	11
Total	1603	966	126	97	36	5	49	13	42	1	76	231	25	16	144	36
% of total present at count	76.3	70.8	6.0	7.1	1.7	0.4	2.3	0.9	2.0	0.1	3.6	16.9	1.2	1.2	6.9	2.6

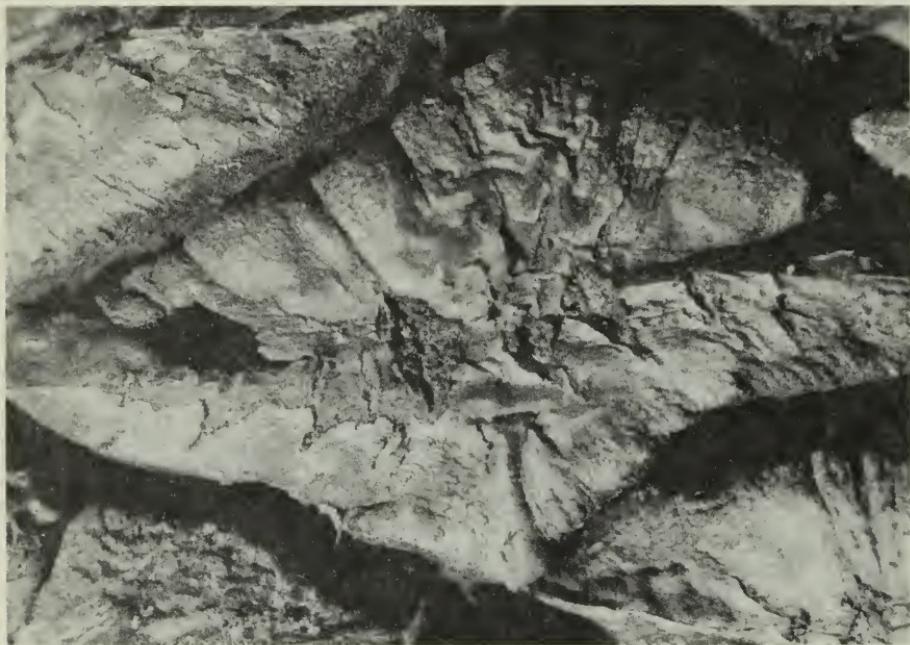


Fig. 51. Giant sequoia cone with emergence hole of *Phymatodes nitidus*.

brown cones sampled. Thus 80% of brown cones were mined in the body of the cone.

Giant sequoia cones remain alive up to 22 years (Hartesveldt et al. 1975). Unless severed from the tree by outside forces such as this beetle, they continue to add tiny annulations to the girth of the peduncle each year.

Adult *Phymatodes* emerge from the cones during early spring and summer, often before the snow has cleared from the groves. Emergence holes may appear anywhere on the cone, but most of them were found on the apical half. The holes were 1.0 to 1.5 mm in diameter and occurred on the flat apophysis of the scales. An emergence hole is illustrated in Fig. 51. Larval density averaged 1.4 individuals per cone in the Castro Tree. A maximum of 8 emergence holes in one cone were found in a tree growing at 2712 meters (8900 ft) in Sequoia National Park. In this tree, at the highest elevation known for the giant sequoia, the emergence holes averaged 4.6 per brown cone, three times greater than the majority of the trees which grow at lower elevations.

The cone count made in August 1970 in the Castro Tree (Table 15) shows the vertical location and incidence of *Phymatodes* activity in cones based on external damage such as emergence holes and the presence of brown cone scales. Experience in rating damage has shown that an error

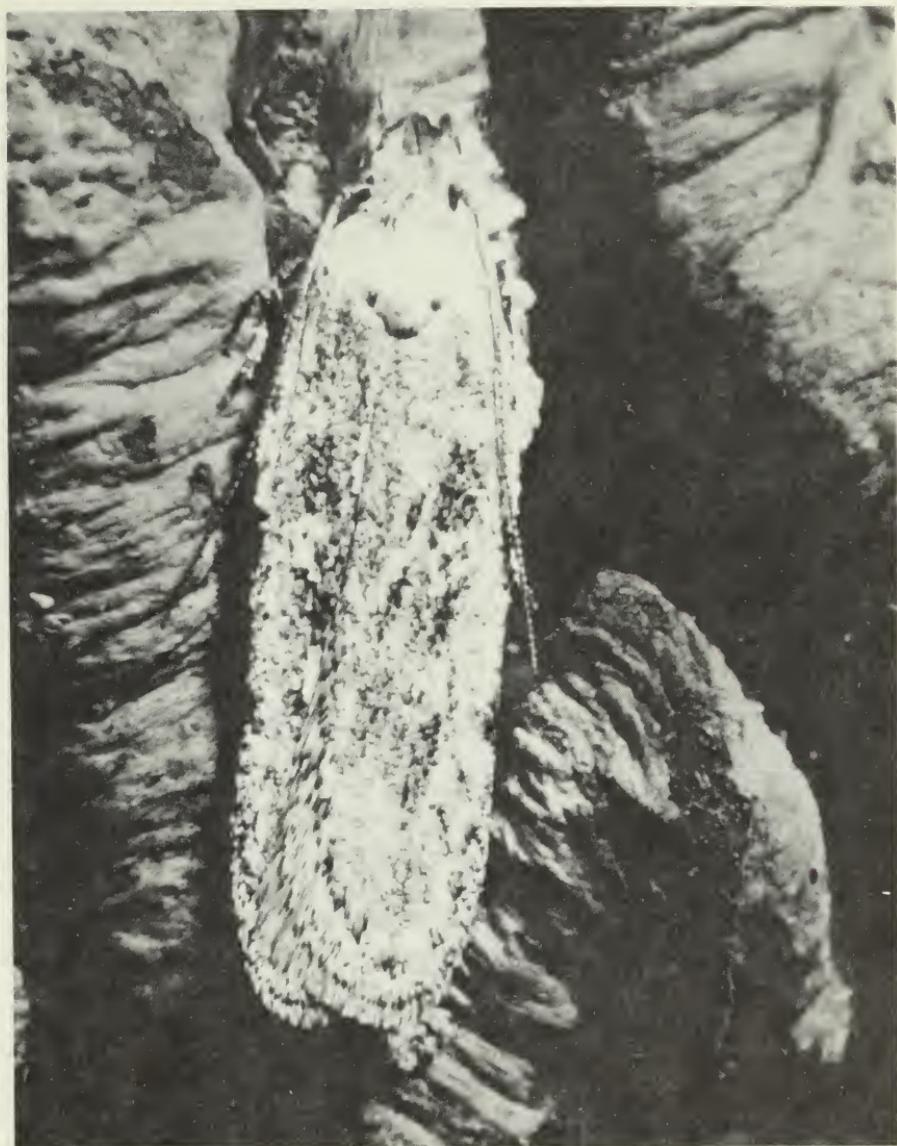


Fig. 52. Adult of *Gelechia* sp.

of as much as 14% was possible in detecting the early stages of *Phymatodes* mining, even if external counts are made late in the summer.

Following the heavy cone crop of 1970 the Castro Tree held a total of 39,508 cones, 70% of which were located in the upper third of the tree. There were 5,948 brown and 20,697 first year cones. Cones of age classes two to twenty years and older numbered 12,836.

**Table 15.** Distribution of ovulate cones and *Phymatodes nitidus* activity in the 290 foot Castro Tree (1970).

Vertical Zones (ft)	Total no. cones per level	P.n. <sup>a</sup> cones per level <sup>b</sup>	Average % P.n. damage
290-280	5212	856	16.4
280-270	4778	1031	21.6
270-260	3290	654	19.9
260-250	5777	1113	19.3
250-240	5361	1349	25.2
240-230	3231	583	18.0
230-220	2136	365	17.1
220-210	1705	293	17.2
210-200	2698	387	14.4
200-190	1089	113	10.4
180-170	560	37	6.6
170-160	2363	116	4.9
160-150	—	0	0.0
150-140	316	10	3.2
140-130	31	4	12.9
130-120	175	7	4.0
120-110	29	1	3.4
110-100	—	0	0.0
100-90	—	0	0.0
90-80	2	0	0.0
80-70	10	0	0.0
Total no. cones	39,508 <sup>c</sup>	6,964	17.6

<sup>a</sup>P.n. = *Phymatodes nitidus*<sup>b</sup>Includes brown cones (killed in past by *Phymatodes nitidus*, less proportioned browned by *Gelechia* (1.2%) and current season's beetle activity involving 1,016 cones in age classes over 2 years.<sup>c</sup>20,697 cones are new cones (1970 had an unusually large crop).

A total of 3,147 brown and semibrown cones were dissected by the double axial-slice technique. *Phymatodes nitidus* mining was found in all age classes examined (Table 16). The cones were selected from the total available in the Castro Tree by self-weighted, stratified random sampling. Over 84% of the attacks occurred in age classes of cones four through nine years. Sixteen brown cones did not show any insect mining and may

**Table 16.** Age classes of 3,147 giant sequoia cones attacked by *Phymatodes nitidus* in the Castro Tree (August 1969).

Age class of cones <sup>a</sup>	Cones with P.n. <sup>b</sup>	Percent of total	Age class of cones	Cones with P.n.	Percent of total
1	0	0.00	11	54	1.72
2	51	1.62	12	81	2.57
3	64	2.03	13	74	2.35
4	308	9.79	14	15	0.48
5	373	11.85	15	3	0.10
6	541	17.19	16	2	0.06
7	507	16.11	17	8	0.25
8	424	13.47	18	1	0.03
9	514	16.33	19	0	0.00
10	122	3.87	20	2	0.06

<sup>a</sup>Age class in years<sup>b</sup>P.n. stands for *Phymatodes nitidus*

be representative of reproductive tissue lost to weather factors, or quite possibly were damaged by the researcher within the tree. The bulk of the cones (34,188 or 86.5%) as well as the *Phymatodes* activity (6631 or 95.2%) occurred in the top half of the foliated portion of the Castro Tree at heights of 60 to 88 m (200-290 ft). A total of 302 cones out of the 3,147 sampled were mined by both *Phymatodes* and a gelechiid moth, *Gelechia* sp.

During the summer of 1968 small gelechiid larvae were noticed boring into giant sequoia cones. They were identified as *Gelechia* sp. by R. W. Hodges of the U.S. National Museum. Unlike *Phymatodes nitidus*, this moth attacks only first year cones and attains the adult stage only about 5% of the time (Fig. 52).

Oviposition by *Gelechia* occurs in first year cones between late June and early August, and takes place at the outside juncture of adjoining cone scales. The fleshy first year cones are relatively soft and apparently provide a feeding substrate for the developing larvae. Resinous cone fluid was exuded at the larval entrance sites on the outer surface of the cone and often trapped early instars of the moth. A three year survey of incidence of new attacks on cones by the moth in the Castro Tree showed a range of from 2 to 27% damage. Differences varied with location on the tree and with the season. A possible correlation between size of cone crop and rate of larval intrusion was illustrated by the fact that in 1968 and 1969, when first year cones occurred in average numbers, 2.6 and 3.5% of the new cones were attacked. In 1970 when the new cone crop

was extremely large, the total moth attack (of new sequoia cones) was 27.3%. Other conifers of Redwood Canyon had similar increase in cone yield in 1970. Table 17 shows the relationship of the 1970 cones attacked by *Gelechia* to elevation in the Castro Tree. Gelechiid incidence was distinctly higher in the upper crown of the tree.

The survival rate of cone feeding *Gelechia* larvae was only slightly higher in low cone yield years than in the extremely heavy cone crop year of 1970. The maturation of larvae was 4.3% in cones in 1969 versus 4.9% in 1970. The number of attacks per cone was easy to distinguish because of the resinous exudate at each entrance point. A mean of 1.7 *Gelechia* entrances per new cone were recorded in the Castro Tree in 1970 with a maximum of five entrances per cone.

Larval mining by this moth differed from that of *Phymatodes* by the presence of silk in the frass, point of entry and the tendency of *Gelechia* to feed within 3 to 4 scales in a group rather than to feed lengthwise along

**Table 17.** Distribution of first year ovulate cones and *Gelechia* sp. activity in the 88 m (290 ft) Castro Tree (1970).

Vertical Zones (ft)	Total no. cones per level	<i>Gelechia</i> cones per level	Average % Cone attack
290-280	3215	1531	47.6
280-270	3168	1349	42.6
270-260	1387	413	29.8
260-250	2921	890	30.5
250-240	2880	627	21.8
240-230	1567	197	12.6
230-220	1429	289	20.2
220-210	960	121	12.6
210-200	1025	174	17.0
200-190	306	41	13.4
190-180	483	22	4.6
180-170	203	6	3.0
170-160	1064	98	9.2
160-150	0	0	0.0
150-140	66	2	3.0
140-130	1	0	0.0
130-120	21	0	0.0
Total no. cones	20,697	5,649	27.3



Fig. 53. Double cone or "twin cones" of giant sequoia induced by gelechiid moth infestation.

the cone axis. Cones first thought to be genetic "doubles" were, on investigation, found to be caused by atypical longitudinal mining in the axial shaft by *Gelechia*. In these cases the shaft split into two lengthwise halves bowed apart in the center, thus giving the double cone effect (Fig. 53). Two samples of 60 and 100 "double cones," when cut open, all showed gelechiid larval damage. None of the several hundred cones observed were completely brown from *Gelechia* activity, with the exception of several undersized defective cones. *Gelechia* may be very numerous in younger sequoia (150–200 ft class). Forty-seven percent of the cones in trees of this size studied in 1974 showed past or present *Gelechia* damage.

Early instars of a small lygid bug were noted feeding upon seeds in newly opened cones. These insects have sucking mouth parts which remove fluid from seeds that have not been dislodged from the open cones. Later growth stages, including the adults of this insect, *Ischnorrhynchus resedae*, retreat deep within the open cone scales when not feeding upon foliage of adjacent new terminals.

## Discussion and summary

### Seedling damage by insects

The differences in observed mortalities through time and between plots can be explained on the basis that those areas experiencing recent disturbances such as burning and/or manipulation appeared to sustain greater insect damage. This parallel between extent of insect damage and a severe disturbance, such as a fire, relates to the earlier observation that under those conditions sequoia seedlings were about the only source of food. Later, as more plants become established, general foliage feeding insects such as the ones reported in this study return to other more desirable plants. The data agree with this hypothesis. Plot 1, established in an eight acre 1965 burn area, showed a significantly greater loss compared to the loss in plots 2 and 3 which were established in an undisturbed forest. The two transects illustrated the same trend where South Area, which burned in 1966 or one year later than Trail, indicated slightly higher seedling loss.

After observing these differences, the decision was made to more closely monitor transects and massed seed beds during the summers of 1969 and 1970. Information was needed to answer questions as to the degree of damage to seedlings short of death, density and differences in damage to seedlings in fresh burn areas versus older and nonburn plots, and the time of year that damage occurred. The 17.5% mortality in the new burn seedling plots (4-13) was almost triple that of prepared seed beds in areas burned two years previously. Plots 14 to 41, randomly selected from within the 1000 foot wide 1970 NPS environmental burn, registered 12.1% mortality due to insects excluding other lesser damage that likely caused mortality at a later date. Field checks of these plots in late summer of 1971 showed loss of 3.4% seedlings to that year's insect activity. Again these data suggest that the largest loss of seedlings came immediately after a burn.

### Release of seed from sequoia cones

The release of seed initiated by *Phymatodes nitidus* activity in the ovulate cones of the giant sequoia is of utmost importance from the standpoint of timing and point of release of seed from the tree. Cones damaged by this beetle will open after drying during the late summer and fall months, which, in effect, may lessen the exposure of the seed to lethal radiation and desiccation. Damaged cones will open several scales at a time over a period of six months to a year. Seed drop was also reported throughout the winter as evidenced by fresh fall on snow (Benner pers. comm.)

It was observed as early as 1967 that seeds falling from the 250 foot level of the Albina Tree would be displaced several dozen meters off the vertical fall line, even on windless days. Winds that accompany late summer Sierran storms strike Redwood Canyon at velocities of from 48 to

64 kilometers (30 to 40 miles) per hour or greater. These storms coincide with fall seed drop from brown cones and cover the forest floor with seeds after every heavy wind. Seeds dropped at this time could be disseminated for at least a quarter of a mile downwind from the parent tree. For example, field tests in the Castro Tree (1969, 1970) showed seeds fall an average 1.8 m (6 ft) per second. Theoretically a wind of 64 kph (40 mph) across the top of the sequoia could move seed 291 m (957 ft) in the first 16.5 seconds in a drop from 85 to 55 m (280 to 180 ft), which is from sequoia crown to the top of the lower canopy of fir, pine and cedar. Additional horizontal movement takes place through this lower canopy at greatly reduced wind speeds. If the wind velocity averages 24 kph (15 mph) (a very low estimate) in a drop from 55 m (180 ft) to the ground, the seed could travel another 210 m (690 ft) in 30 seconds of descent, or a total dispersal of 502 m (1647 ft) lateral displacement. This dispersal of well over 0.4 kilometers (one-quarter mile) need only occur once in every 100 years or more for sufficient reproduction but probably happens several times a summer and with even greater frequency in winter.

Measurement of vertical and lateral seed motion in a uniform airstream is acceptable only in gaining averages for seed dispersal in the many variable sites and tree configurations. Factors such as gustiness and updrafts caused by cover turbulence affect vertical range of drop (Kittridge 1948).

### Relationship and role of cone insects to other reproductive forces

The two principle cone insects avoid competition with each other by feeding on different year classes. *Phymatodes nitidus* mainly mines cones of age classes four years and older while the cone boring moth, *Gelechia*, feeds only upon the first year cones (damage may cause some seeds to be released through the second or third year). Such a relationship of sequential feeding is not unique. Coulson and Franklin (1968) found similar selective behavior with *Dioryctria* coneworms and cecidomyiid cone maggots, which attacked 14.3% of the second year cones of the shortleaf pine, *Pinus echinata*. They noted that fresh first-year cones were not mined by *Dioryctria*, while dried first-year cones were fed upon by the gelechiid, *Battaristis vitella*. The latter could not be induced to feed on living cones.

Lichens begin to grow on the exterior surface of the sequoia cones at about the time that *Phymatodes nitidus* activity and the optimal seed viability of the giant sequoia diminishes. Such growth may prevent the seeds from falling free of the cones (Fig. 54). Two species of lichens may completely cover individual cones or, in some cases, completely conceal entire cone masses. The predominant lichens growing on cones in the age classes beyond eight years are *Parmelia physodes*, a foliose form; *Letharia vulpina*, a chartreuse dendritic form; and *Hypogymnia imshangii*, a black

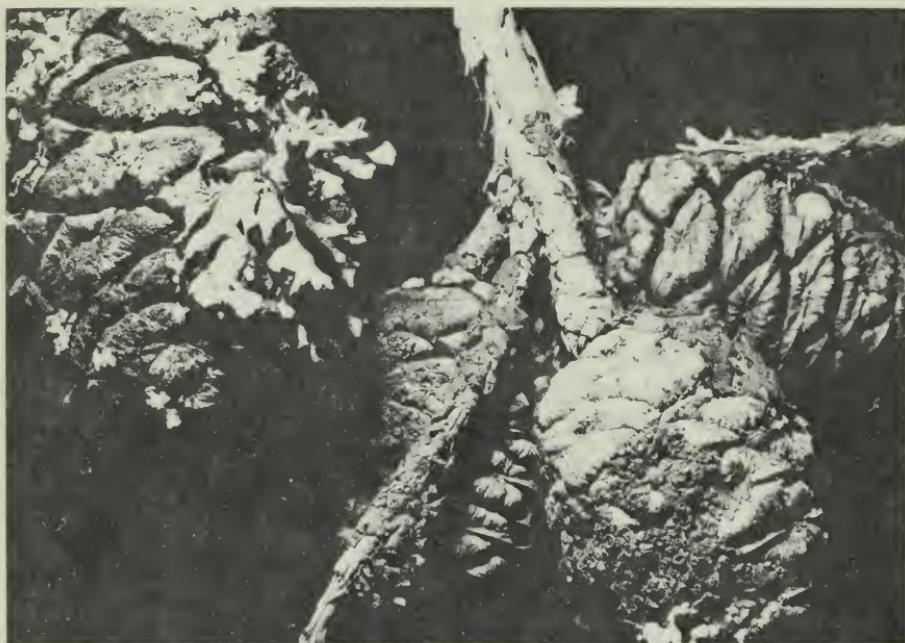


Fig. 54. Lichen covered cones of a giant sequoia.

and white inflated lobe type. Small specks of lichen growth usually appear prior to eight years but probably do not impede seed drop.

Several physical factors may aid in cone release and subsequent dispersal. The more important factors include snow loading of branches, ice deposits from ice storms, and heavy winds which may cause an increase in the drop of cones and may be of sufficient magnitude to release many seeds possessing strong attachment to the open cones. Seeds of this type examined from the top of the Castro Tree in 1969 and 1970 showed that 75% (by snap test) were viable, which is unusually high for sequoia seed (Chapter 5).

Fire is the most important physical agent concerned in reproduction of the giant sequoia, as was discussed in Chapter 5. Super-heated air may cause death of the cones with resultant release of large quantities of seed.

In summary, insects rarely attacked the 1-2 year old seedlings of giant sequoias except where they grew in dense numbers. The cone insects are also few in number, namely a moth that damages first year cones and a minute beetle that causes cones to drop their seeds. The latter insect is very important in the continual release of seeds and subsequent reproduction of the giant sequoia.

# Birds and Mammals, Fire, and Giant Sequoia Reproduction

Howard S. Shellhammer

## Introduction

Giant sequoia groves do not possess a special vertebrate fauna. The fauna of the groves varies with altitude and latitude, just as it does in the mixed coniferous forest that surrounds them and which runs the length of the Sierra Nevada.

The mammals of the Redwood Mountain Grove are dominated by rodents: deer mice (*Peromyscus maniculatus*), Douglas squirrels (*Tamiasciurus douglasi*) and to some degree by California ground squirrels (*Otospermophilus beecheyi*) and chipmunks (*Eutamias* spp.). A listing of the other mammals, amphibians and reptiles, all common to much of the Sierra Nevada, can be found in Hartseldt et al. (1975). Wallis (1951) reported on vertebrates in the Mariposa Grove. An extensive list of the breeding birds in one portion of the Redwood Mountain Grove was compiled by Kilgore (1971a) and is applicable to our present study areas. Dominant species include the dark-eyed junco (*Junco oreganus*), mountain chickadee (*Parus gambeli*), robin (*Turdus migratorius*), black-headed grosbeak (*Pheucticus melanocephalus*), western tanager (*Piranga ludoviciana*), western wood peewee (*Contopus sordidulus*), and red-breasted nuthatch (*Sitta canadensis*).

Few studies have been carried out to determine the relationship between fire and the birds and mammals of the groves. Kilgore (1971) studied the changes in the numbers of breeding birds in Whitaker's Forest following manipulations similar to the present study. Whitaker's Forest, a 130 hectare (320 acre) experimental forest of the University of California on the western slope of Redwood Mountain, is located within the boundaries of the Redwood Mountain Grove (Fig. 3).

Little information other than conjecture has been made as to which birds and mammals interact directly with the giant sequoia or affect its reproduction. Ingles (1965) and Fry and White (1930) noted that Douglas squirrels cut and cached giant sequoia cones and also inferred that they consume their seeds. Fry and White (1930) presented no figures but gave the following description of seedling-animal interactions:

Among the conifers I know of no other that is attacked in infancy by so many destructive agencies as the Big Tree. No sooner are the seedlings above the

ground than destruction and disaster assail them, so that few survive the first year. Birds, such as sparrows and finches, are attracted to the tender green plants with their seed hulls on their tops and pick off the topmost portion for food. This invariably kills the plants. Cutworms destroy many of the plants by cutting them off near the ground. Large blackwood ants levy a heavy toll by cutting off the plants and dragging them to their nests. Rodents, such as ground squirrels and chipmunks, destroy many of the plants by eating off the tender tops.

The acceptance of some of these generalizations must be tempered by the fact that many of the observations were made in nursery conditions outside of a grove, where seedling sequoias were being grown in thick beds.

The present study attempts to ascertain whether the vertebrate interactions described by Fry and White (1930) are correct and to gain some idea of the magnitude of the effect of birds and mammals on sequoia reproduction. It also attempts to identify the changes taking place in the number of birds and mammals following the use of fire and associated manipulations in a grove. This study dwells upon the impact of birds and mammals on the seed and seedling stages of the giant sequoia.

## Methods

Most of the studies reported on in this section took place in Ridge, North and Trail Areas (Chapters 2 and 3 for descriptions, Fig. 4). Miscellaneous investigations took place in and near the Redwood Mountain and General Grant Groves of Kings Canyon National Park and the Giant Forest of Sequoia National Park (Fig. 3).

### Avian studies

Populations of some of the species of breeding birds, in both the manipulated and control portions of Ridge, North and Trail Areas were measured in 1965 and 1966 by the plot census method (Kendeigh 1944), using dittoed maps on which to record observations. This same method was used by Kilgore (1971a) in studying bird populations on the other side of Redwood Mountain during the same years. Routes were taken through the study areas such that the observer came within 30.5 m (100 ft) of every point in each area. Activities of all birds were recorded, with special emphasis given to singing males. Five censuses were made between late June and early August in 1965 and again in 1966. Approximate territories or areas of activity were identified at the end of the season by circling groups of observations on the dittoed maps.

## Mammalian studies

Small mammals were trapped using mouse and rat-sized Sherman live traps in both the manipulated and control portions of North Area in 1964, and in Ridge, North and Trail Areas in 1965, 1966 and 1967 for a total of 5527 trap nights (Fig. 55). Captured mice and chipmunks were tagged with numbered ear tags, measured, checked for sexual condition, and released. Each area was trapped between five and eight times per summer. The density of mice per area was calculated using the technique developed by Brant (1962) of adding a border to the trapping area equal to the average distance moved of the animals in that population for that particular trapping period.

Chipmunks, ground squirrels and Douglas squirrels were censused using the plot census method developed for birds by Kendeigh (1944). The method was modified to include long periods of direct observation from fixed points. None of these larger rodents were ear-tagged. Chipmunks and ground squirrels were censused from 1965 through 1967 and Douglas squirrels from 1965 through 1967 (Chapter 9) for a total of approximately 650 hours of observation.

Deer and other large mammals, such as coyotes and grey foxes, were observed, or the evidence of their activity was noted in the censusing mentioned previously or during the many hundreds of other hours spent in or near the study areas.

## Seed preference studies

Seed preferences were checked using a modification of the seed spot method which Tevis (1956) modified from Moore (1949-50). Seeds of seven conifers, as well as sunflower, were buried in 1.3 cm (0.5 in) deep pits spaced 60 cm (24 in) apart in cleared areas on the forest floor. Generally eight pits, one of each kind of seed, were used in each experiment, which yielded 4.5 meter by 60 cm cleared areas. Fifteen of each type of seed, except giant sequoia seeds where 45-50 were used, were buried in each pit. The sequence of seeds (pits) in an experimental area was randomly rearranged if more than one series of tests were run in an area during the summer. Thirty-five series (278 pits) were run in the Redwood Mountain Grove in 1965, as were 31 series (249 pits) in 1966. Ten series (80 pits) were run in a non-sequoian, mixed conifer forest near the Grant Grove in 1965. Conifer seeds included sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), red fir (*A. magnifica*), incense cedar (*Calocedrus decurrens*), and giant sequoia. Jeffrey pine and red fir were not found in the test areas. All conifer seeds used were collected by the California Division of Forestry from areas close to the Redwood Mountain Grove. The activities of various species of rodents were easily discernible. Deer mice dug simple, neat pits over the seed spots while chipmunks and Douglas squirrels

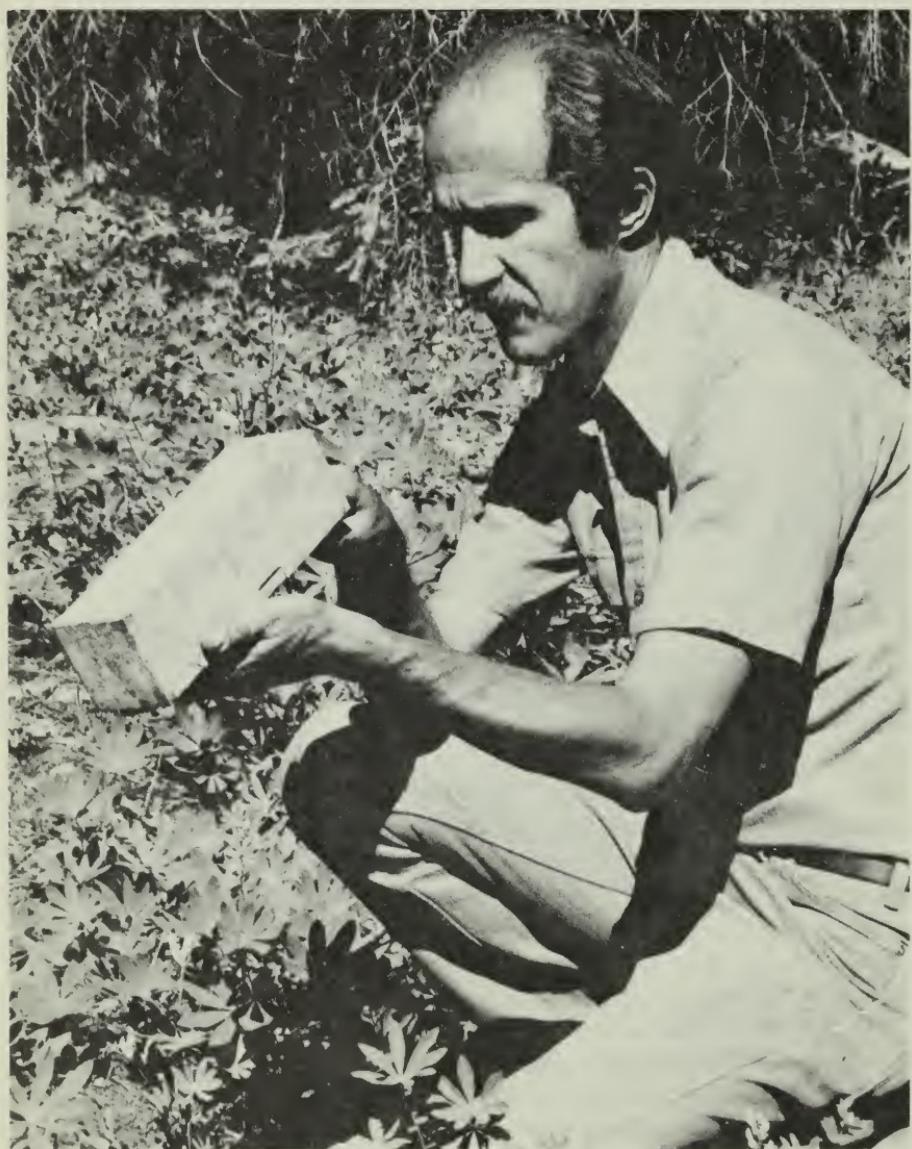


Fig. 55. Live trap held by Howard Shellhammer.

undertook considerable exploratory digging and made larger pits. Birds did not uncover seeds buried in this manner.

### Seedling studies

All seedlings germinating and observable in the manipulated areas were marked and observed for animal damage during the period of the study or until they died (Chapter 5 for seedling mortality studies). Stecker (Chapter 6) estimated the loss of seedlings to insects in various plots and in transects both in and outside of the study areas.

Seedlings of giant sequoias, incense cedars, Jeffrey pines, and red firs were grown in  $40.6 \times 20.3 \times 15.2$  cm boxes in a greenhouse at San Jose State University in San Jose, California, and the boxes were placed in the treated and control portions of North and Trail Areas in early July 1966. Observations were made on the fate of 174 seedlings ranging from 1–2 cm giant sequoias to 7–19 cm red firs from July 4 to August 15, 1966.

## Results

### Avian studies

The territories of only seven species of birds, plus the empidonax complex of flycatchers, could be assessed with certainty due to the lateness of the observation periods in both years (Table 18). Empidonax flycatchers increased slightly in the control plots and decreased in the manipulated plots in North Area. Mountain chickadees increased in both plots in Ridge but not in North Area. Dark-eyed juncos showed only a slight decrease in treated versus control plots, whereas western wood peewees increased in the treated areas. A noticeable, but unsubstantial, increase in the number of robins occurred in the treated areas. These results were similar to those obtained by Kilgore (1971a) in 18.2 hectare (40 acre) manipulated and control plots in Whitaker's Forest during the same years (1965 and 1966). Both studies showed similar changes in empidonax flycatchers, mountain chickadees, western wood peewees, and robins, while Kilgore noted a larger decrease in dark-eyed juncos in treated plots. Relatively small and similar changes in avifauna were observed in our small manipulated areas (approximately 2 hectares) and the 18.2 hectare areas studied by Kilgore. The type of habitat manipulations in both studies were generally similar.

Apparent sapsucker damage was observed on the upper portions of nearly all the larger giant sequoias inspected (Fig. 56). Such damage is attributed to sapsuckers because of the characteristic pattern of holes in the thinner portions of the bark, even though no researchers, past or present, have seen sapsuckers working the trees. A survey of 32 trees in and near South Area showed that all but two of the 26 trees with a diameter at breast height (dbh) of 1.8 m (4.5 ft) or larger had moderate to extensive

**Table 18.** Numbers of pairs of birds per hectare in Ridge, North and Trail Areas before and after manipulation and burning.<sup>a</sup>

Feeding height and species	Ridge Area				North Area				Trail Area	
	Control 1965 1966		Burn 1965 1966		Control 1965 1966		Burn <sup>b</sup> 1965 1966		Preburn 1965	Postburn 1966
<b>UPPER CANOPY</b>										
<i>Empidonax</i> sp.	0	0	0	0	2	3	1.5	0.5	0.5	0.5
Western tanager	1	1	1	1	1.5	1	1	1	0.8	0.5
<b>UNDERSTORY</b>										
Western wood peewee	0	1	1	1	0	0	1	2	0.5	0.5
Mountain chickadee	2	3	1	3	1	1	1	1	0.5	1
<b>BRUSH/SAPLING</b>										
Winter wren	0	0	0	0	1	0	0	1	0.5	1
Townsend's solitaire	0	0	0	0	0	0	0	0	0.5	0
<b>TRUNK GROUND</b>										
Hermit thrush	0	0	0	1	0	0	0	0	0.3	0.5
Black-eyed junco	2	1.5	1	1	4	5	4	4	1.5	1.0

<sup>a</sup>Ridge and North Areas had controls while Trail Area did not.

<sup>b</sup>1965 burn area in North Area was partially manipulated in the fall of 1964 and was burnt again in the fall of 1965, hence 1965 is really postmanipulation #1 and 1966 is postmanipulation #2.

All areas listed are about 1 hectare except Trail which was approximately 2 hectares.

drilling damage on the upper two-thirds of their trunks. Much of this damage appeared to be old, but no estimate could be made of how old. Trees with a dbh of less than 1.8 m (4.5 ft) seldom showed such damage. A similar situation existed in the other study areas.

Stecker (Chapter 7) noted sapsucker damage near the top of the large giant sequoia in which he worked in 1968. He noted that it was extensive enough to impair vascular transport and apparently was resulting in the retardation of growth of the leader shoot of the tree.



Fig. 56. Apparent sapsucker damage on the trunk of a giant sequoia.

### Mammalian studies

Deer mice (*Peromyscus maniculatus*) were the most common mammals in the study areas (Fig. 57). They were most numerous in 1965 but declined each year for the next two years (Table 19, Fig. 58). Approximately two



Fig. 57. A deer mouse, *Peromyscus maniculatus*, tagged in the ear with a light-weight, numbered tag.

times as many mice were trapped in the treated versus control portions of North Area in 1966 and 1967 and Trail Area in 1966. There were, however, slightly more mice in the control portion of North Area in 1965, a fact possibly associated with the sequence of manipulations of that area. North Area was first manipulated and partially burned in the fall of 1964, but the fire did not carry well due to the mechanical disturbance of the litter surface. The piles of logs were reburned in the fall of 1965.

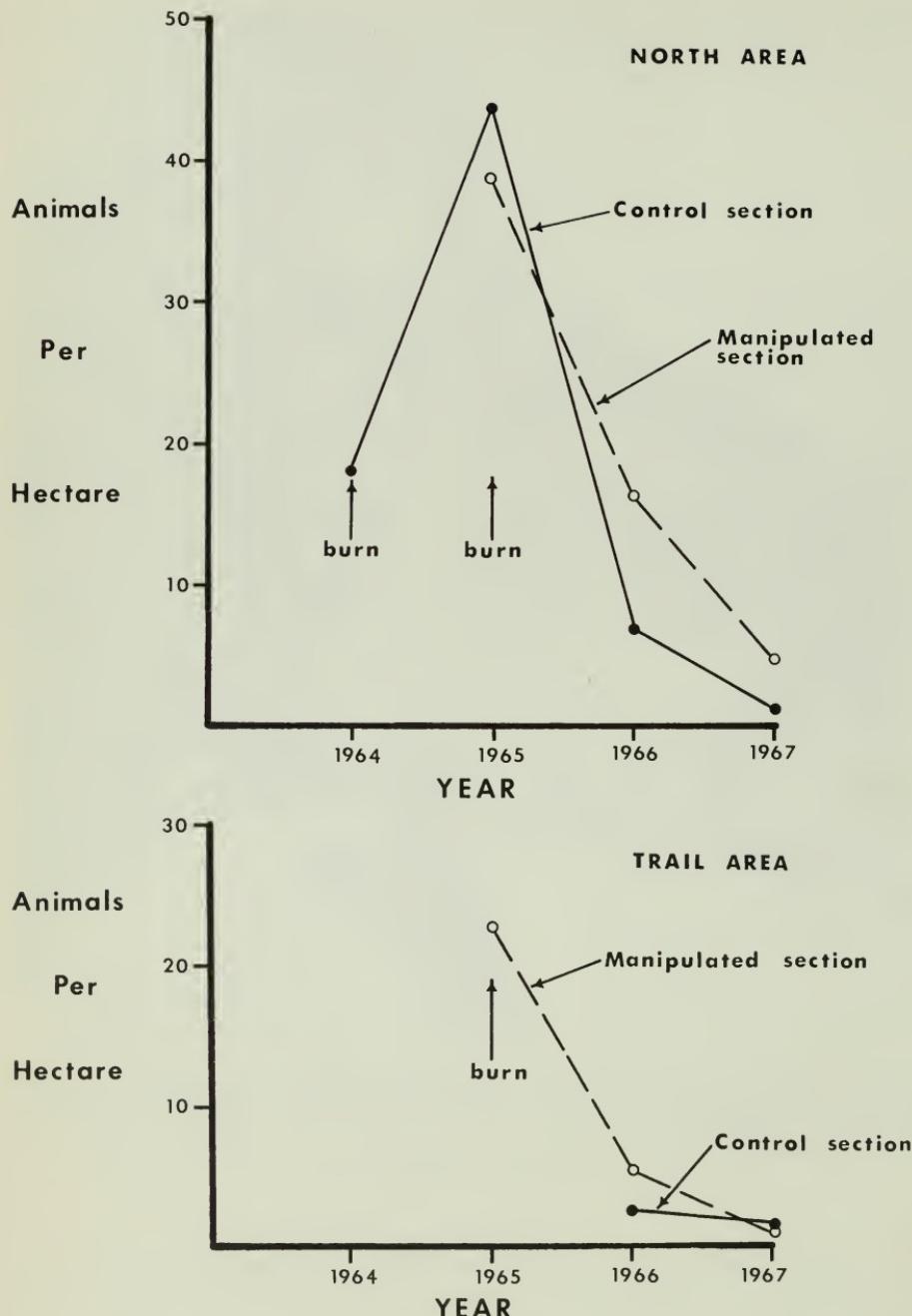
**Table 19.** Numbers of deer mice, *Peromyscus maniculatus*, in North and Trail Areas before and after manipulations.

Year	Animals captured twice or more	Adjusted area in hectares <sup>a</sup>	Density in hectares	Av. D. <sup>b</sup> in meters
<b>North Area CONTROL</b>				
1964	20	1.1	18.0	21.5
1965	34	0.8	43.7	13.7
1966	23	3.4	6.7	30.7
1967	6.5	4.8	1.2	69.6
<b>North Area MANIPULATED</b>				
1964	—	—	—	—
Burnt in fall of 1964				
1965	36	0.9	38.7	13.7
Piles reburnt in fall of 1965				
1966	15	0.9	16.1	30.7
1967	4.5	0.9	4.9	73.8
<b>Trail Area CONTROL</b>				
1964	—	—	—	—
1965	—	—	—	—
1966	4	1.7	2.5	27.6
1967	5	3.0	1.7	58.6
<b>Trail Area MANIPULATED</b>				
1964	—	—	—	—
1965	45	1.9	22.7	14.2
Burnt in fall of 1965				
1966	15	2.7	5.4	27.6
1967	5	4.3	1.2	56.7

<sup>a</sup>Area is adjusted by adding a band equal to the average distance moved between captures of animals in that population.

<sup>b</sup>Av. D. is average distance moved between captures.

The reproductive activity of these mice was high in 1965 when an estimated 184 young were added to North Area during the time of the summer study period. Fewer of these young animals were trapped than expected. There was no evidence of emigration, as there was in 1966 in

Fig. 58. Densities of *Peromyscus maniculatus* in North and Trail Areas.

the same area. One male of the smaller 1966 population moved 400 meters (1,320 ft) down the canyon to near Trail Area. The implications of such a move in relationship to emigration is grossly conjectural because of the single observation. In addition, the average distance moved between captures, Av.D. (Table 19), was inversely related to density, with the Av. D. being the smallest in 1965. Predators such as coyotes and owls were associated with the areas, however the coyote scats examined contained few remains of mice. The effects of the owls and other birds of prey on mouse populations were not considered in this study.

The squirrels and chipmunks present included the grey squirrel (*Sciurus griseus*), Lodgepole chipmunk (*Eutamias speciosus*) and Townsend's chipmunk (*E. townsendii*) in addition to the Douglas squirrels and California ground squirrels mentioned earlier. The numbers of the other species increased in 1966 and dropped in 1967 (similar to, but not as dramatically as did the Douglas squirrels). There was little difference in their numbers between the treated and control portion of the study areas, although such distinctions were made difficult by the relatively small sizes of the plots.

A grey squirrel inhabited part of North Area in 1965 and 1966, and another was observed in Trail Area from 1965 to 1967, as well as in later years of the study, when squirrels other than the Douglas squirrel were receiving little attention. One dug up two sequoia cones in Trail Area in 1966 and ate on them in a manner similar to that used by Douglas squirrels (Chapter 9). The cones were partially trimmed by this animal, and one of them was reburied. It is doubtful that these cones were previously cached by Douglas squirrels because the site was too open and the soil was too dry. Grey squirrels ate sugar pine cones, often just before the time of the year that Douglas squirrels started to cut them. This was especially true in the late summer of 1974 when there were few Douglas squirrels, and most conifers, excluding giant sequoias, had very few cones on them. Several groups of sugar pines which had moderately good cone loads were stripped of their cones by grey squirrels, and the cones were then eaten near the bases of the trees. No instances were observed of grey squirrels cutting or caching giant sequoia cones except for the instance previously mentioned. Grey squirrels may have eaten some fallen sequoia cones, but the number was insignificant compared to the numbers cut by Douglas squirrels (Chapter 9).

A California ground squirrel was observed to eat part of a Jeffrey cone at a site two kilometers upslope from Ridge Area, but that was the only incidence of that species feeding on cones during the term of the study. No observations were made of this species eating any giant sequoia materials.

Trowbridge shrews (*Sorex trowbridgii*) were present in North and Trail Areas in low numbers (1 to 4 animals) in 1965 and 1966. One mole (*Scapanus latimanus*) was known to be present in North Area in 1966. While

their diggings were not seen, pocket gophers (*Thomomys bottae*) were observed in the talons of goshawks as they moved through North and Trail Areas on several occasions in 1965 and 1966. One meadow mouse (*Microtus longicaudus*) was captured in North Area in 1965, and two were captured in 1966. Several small white firs in the control portion of North Area were partially girdled (one killed) by meadow mice in the winter or early spring of 1965–66. A meadow mouse was observed in the same area in the summer of 1966 eating the tips of small white firs. No damage positively attributable to meadow mice was observed on any giant sequoia.

### Seed preference studies

Giant sequoias shed enormous numbers of seeds. My best estimate is 180 seeds/m<sup>2</sup>/yr under mature trees while Harvey (Chapter 5) noted a variation on the ground of a few dozen to several thousand seeds/m<sup>2</sup>/yr. The former figure was arrived at by multiplying the number of seeds per cone (200) times the average number of cones shedding seeds per tree per year (1,500) times the number of mature trees per hectare (6) divided by 10,000 (i.e. m<sup>2</sup>/ha). Such shed seeds were considered initially to be a potential food source for the animals of the grove.

Seed preferences of various rodents, as tested in the seed spot tests, are listed in priority order on Tables 20 and 21. Chipmunks, and possibly a few Douglas squirrels, accounted for 60% of the seed spots uncovered in 1965 and 95% of those uncovered in 1966. Deer mice accounted for the difference each year. The variation between years is correlated with rodent densities. Deer mice were four times more plentiful in 1965 in trapping grids near the seed spot test sites than in 1966 (Table 19). Chipmunks and Douglas squirrels were both twice as numerous in 1966 as in 1965 (Chapter 9, Table 24).

Large pine seeds were the preferred type of food each year, regardless of whether they were native to the area of the test or not. Sunflower seeds were also highly desired. They were successfully used as bait in trapping small mammals in areas away from the seed preference sites. Giant sequoia seeds were the least preferred, apparently because they were the smallest in size and weight, and were partially eaten in only 14% of the spots inside the grove and 19% of the spots outside in 1965 (Tables 20, 21). Eight of the nine spots partially eaten that year were eaten during the first run at any particular site. All of the spots of sequoia seeds were exposed but not eaten during the second run one week later at the site outside the grove, while approximately 50% of the spots inside the grove were not exposed at all, and only one was exposed and partially eaten. Ninety-four percent of the spots of giant sequoia seeds were uncovered but not eaten in 1966. Rodents generally preferred large seeds, although the highly preferred ponderosa pine seeds were relatively small (Table 22).

**Table 20.** Preference of rodents in 1965 seed spot tests at Redwood Mountain Grove and near Grant Grove.

Redwood Mountain Grove						
Rank	Seed	Percent exposed, eaten	Percent exposed, partially eaten	Percent exposed, not eaten	Percent not exposed	No. of tests
1	Sugar pine	100.0	—	—	—	25
2	Ponderosa pine	100.0	—	—	—	25
3	Jeffrey pine	100.0	—	—	—	25
4	Sunflower	100.0	—	—	—	25
5	White fir	91.0	9.0	—	—	35
6	Red fir	72.0	28.0	—	—	25
7	Incense cedar	25.5	43.0	25.5	6.0	59
8	Giant sequoia	—	14.0	43.0	43.0	59

Near Grant Grove <sup>a</sup>						
Rank	Seed	Percent exposed, eaten	Percent exposed, partially eaten	Percent exposed, not eaten	Percent not exposed	No. of tests
1	Sugar pine	100.0	—	—	—	8
2	Ponderosa pine	100.0	—	—	—	8
3	Jeffrey pine	100.0	—	—	—	8
4	Sunflower	100.0	—	—	—	8
5	Red fir	100.0	—	—	—	8
6	White fir	88.0	12.0	—	—	8
7	Incense cedar	44.0	31.0	26.0	—	16
8	Giant sequoia	—	19.0	81.0	—	16

<sup>a</sup>Outside of Grant Grove in a mixed coniferous forest.

**Table 21.** Preference of rodents in 1966 seed spot tests at Redwood Mountain Grove.

Rank	Seed	Percent exposed, eaten	Percent exposed, partially eaten	Percent exposed not eaten	Percent not exposed	No. of tests
1	Sugar pine	96.6	—	—	3.4	29
2	Ponderosa pine	92.0	—	—	8.0	25
3	Sunflower	92.0	—	—	8.0	25
4	Jeffrey pine	88.0	—	—	12.0	25
5	Red fir	56.0	28.0	12.0	4.0	25
6	White fir	37.9	48.3	13.8	—	29
7	Incense cedar	—	15.8	71.1	13.2	38
8	Giant sequoia	—	—	94.3	5.7	53

**Table 22.** Seed preference of rodents versus average seed weight.

Rank	Seed	Weight of seeds in grams					
		0.20	0.15	0.10	0.05	0.01	0.005
1	Sugar pine	0.22					
2	Ponderosa pine				0.05		
3	Sunflower			0.10			
4	Jeffrey pine			0.12			
5	Red fir			0.09			
6	White fir				0.04		
7	Incense cedar					0.03	
8	Giant sequoia						0.005

**Table 23.** Damage to laboratory-grown seedlings placed in study areas.

Species and size	N	Number damaged	Type of damage
Giant sequoia, 1-2 cm	18	2	1 eaten by insects, 1 unearthed
Giant sequoia, 2-4 cm	48	22	5 crushed by deer, 5 chewed on by insects but not killed, 12 topped and killed by insects or birds
Giant sequoia, 4-6 cm	62	10	10 dug up by rodents
Incense cedar, 5-7 cm	21	0	—
Jeffrey pine, 12-14 cm	15	0	—
Red fir, 7-19 cm	10	0	—

### Seedling studies

Desiccation accounted for 84.6% of the mortality in 5206 marked seedlings (see seedling mortality studies, Chapter 5). Insects caused another 5.7%, while birds and mammals killed 1.1% of the total. Included in those killed by birds and mammals were three seedlings trampled by deer and 15 crushed by horses. No fatal damage caused by birds, mammals or insects was observed in seedlings older than three years (Chapters 5 and 7).

Stecker's studies outside the study areas (Chapter 7) revealed much the same pattern. He reported slight loses to deer browse in first year seedlings.

No damage to deer browse was noted on older giant sequoia seedlings or young trees, although *Ceanothus parvifolius* and other shrubs both inside and out of the study areas were browsed in various years. A few four and five year old giant sequoia seedlings were browsed by deer in an area manipulated by the park service on the ridge of Redwood Mountain.

Moderate damage to boxed seedlings can be attributed to birds or mammals. Twelve of the 48 2-4 cm giant sequoias killed during the period of observation were killed either by insects or birds (Table 23). Insects are suspected in this case, as five other seedlings in a nearby box were chewed upon by insects but not killed. A tight bunch of five seedlings were crushed by a deer as it moved through the area of the boxes. Ten of the larger seedlings were dug up, and the box in which they were growing was partially displaced, presumably by California ground squirrels which had

their den close by. None of the largest giant sequoia seedlings (4–6 cm, Table 23) were eaten by vertebrates, although some were dug up, as mentioned above. Thus twenty-five percent (32) of the 128 boxed sequoia seedlings were killed during the test, with the heaviest damage in the intermediate size group (2–4 cm).

One pertinent direct observation was made in 1966 of the interaction of a female purple finch and several boxes of seedlings. The bird spent several minutes moving through the boxes pecking at the surface of the soil between seedlings. None of the seedlings were eaten by the finch.

## Discussion

### Effects of fire on birds and mammals

Experimental burns of two to four hectares produced relatively minor changes in bird and small mammal populations. These small burns resulted in decreases in empidonax flycatchers and dark-eyed juncos and increases in western wood peewees and robins. Similar results were observed by Kilgore (1971) in larger (18.2 hectare) burns. The dominant small rodent, *Peromyscus maniculatus*, was 2.1 to 2.4 times more numerous in burned areas than in control areas in the year following the burn. Similar increases after burns of various sizes have also been described by Alhgren (1966), Cook (1959), Garman and Orr-Ewing (1949), Gashwiler (1970), and Tevis (1956). The numbers of Douglas squirrels appeared to be affected by other factors than those resulting from fires (Chapter 9).

Bendell (1974) summarized numerous studies and observed that most populations (80%) of birds and mammals studied showed no significant changes after fires. He noted a similar stability in the number of species remaining in forests after fires. This is in large part a result of the fact that direct mortality due to fire is small (Hakala et al. 1971; Howard et al. 1959; Komarek 1969; Vogl 1973). Bendell also noted that most fires burn unevenly, leaving a mosaic of successional stages in the forest, seldom producing large uniform areas of uniform vegetation. Such mosaic forests provide a variety of environments and wildlife as well as colonists to new burns (Daubenmire 1968; Heinselman 1970; Vogl 1970). While the present studies involved burns of too small a size to test these ideas, future consideration should be given to maintaining the mosaic features of giant sequoia and associated mixed coniferous forests as larger management burns are used.

A number of changes in bird and mammal populations are forecast if fire is reintroduced in the groves on a larger scale. Larger and potentially hotter fires kill more white fir and potentially more sugar pine, the former to heat and the latter to insects. The resultant increase in wood-burrowing insects will result in increased numbers of trunk-feeding birds for several years. This should also result in an increased number of flycatchers and

woodpeckers. The magnitude of such changes can be reduced if the burns are kept from becoming much hotter than the experimental burns. The number of Douglas squirrels should not be affected appreciably, while the numbers of California ground squirrels are expected to increase. The latter species is a ground-dwelling form which favors open, well-lighted conditions and which has been noted to increase after logging and burning (Gashweiler 1970; Tevis 1956). The magnitude of the changes in bird and mammal populations will depend on how far back the successional process is pushed by the manipulations, and on the pattern of burning used in treating larger areas of the groves.

### Birds, mammals, and giant sequoia reproduction

Birds and mammals exert little effect on giant sequoia seeds either on the ground or on seedlings. The principal reason for this seems to be their small size. A seed weighs but 0.005 gram, and an average of only about 180 fall to each square meter of ground per year. Even then, however, only 5 to 10 seeds fall per day, which is a very low return in food energy for the energy expended gathering, eating and assimilating them. The seed spot tests showed few sequoia seeds were used even when concentrated in groups of fifty seeds. Preference was given by the rodents to the largest seeds in all cases. There is evidence that the animals learned not to spend time on sequoia seeds and to search for larger seeds. Those sequoia seeds eaten were consumed during the first series of tests at a particular site. They were either not uncovered or uncovered but not eaten during the second series at each site, presumably by the animals that visited the site previously. Harvey (Chapter 5) and Stecker (Chapter 7) showed that most seeds on the ground died of desiccation or by insect attack. Douglas squirrels eat some seeds in the cones and cause the shedding of many more.

Few giant sequoia seedlings are eaten by vertebrates. Concentrated masses of these seedlings seldom provide enough biomass to be of interest to an herbivore. There was a higher mortality in boxes of seedlings (25%) than in those seedlings that germinated naturally in the study areas (approximately 1%), presumably because of the differences in their density. Deer occasionally browsed dense groups of seedlings, a phenomenon also noted by Stecker (Chapter 7). Such browsing was haphazard, and the animal usually moved on after a few bites. Some seedlings were crushed by various mammals. Birds do take a few seedlings, again more often when the seedlings grow in dense clusters. This tendency helps explain the views of Fry and White (1930), who suggested that vertebrates have a considerable impact on giant sequoia seedlings after having observed numerous interactions in a nursery setting.

Birds and mammals killed only 1% of the marked seedlings dying from all causes. Their effect was greatest when the seedlings were one to two

years old, and especially when they were concentrated in dense groups. Some insects have specialized to support themselves, at least in part, on the small amounts of food energy found in the seeds and young seedlings (Chapters 6 and 7). No bird or mammal is apparently so specialized.

# Douglas Squirrels and Sequoia Regeneration

Howard S. Shellhammer

## Introduction

John Muir (1911) said of the tree squirrels of the Sierra Nevada:

There are two species here, the large California gray and the Douglas. The latter is the brightest of all squirrels I have ever seen, a hot spark of life, making every tree tingle with his prickly toes. . . a condensed nugget of fresh mountain vigor and valor. . . .

The Douglas squirrel (*Tamiasciurus douglasii*) (Fig. 59) plays a significant role in the life history and regeneration of the giant sequoia as does no other vertebrate (Chapter 8). Earlier reports emphasized the cone cutting and caching activities of these squirrels (Cahalane 1942; Clarke 1939; Fry and White 1930; Ingles 1965; Murie 1927). Subsequently, Fry and White (1930) and Shellhammer (1966) documented that Douglas squirrels cut large numbers of giant sequoia cones. Fry and White suggested that one squirrel cut and cached "thirty-eight well-filled barley sacks of cones. . . within a period of about twelve days," while Shellhammer (1966) observed one squirrel cut 538 cones from one giant sequoia in 30 minutes. Speculation has prevailed as to the extent that this sort of behavior is common to Douglas squirrels inhabiting sequoia groves, but no detailed studies had been conducted, prior to the present study, to explore this subject.

Earlier investigations inferred or believed that Douglas squirrels ate upon giant sequoia cones solely to gain seeds from them, as they do with all other conifer cones (Fry and White 1930; Ingles 1965). The present author questioned this supposition because of the extremely small size of giant sequoia seeds and the green fleshiness of the cones. Hartesveldt and Harvey (1967) reported that it takes an average of about 200,000 seeds to weigh a kilogram (91,200 seeds per pound), each seed (including seed coats and wings) weighing approximately 0.005 gram (Fig. 60). The two hundred seeds in an average cone (Chapter 5) would yield but one gram potential food for the 15 to 30 minutes of effort required to obtain it. Most investigators also assumed that the behavior and biology of Douglas squirrels inside groves of giant sequoias is much like that reported for them elsewhere throughout their range.



Fig. 59. A Douglas squirrel, *Tamiasciurus douglasii*.



Fig. 60. Seeds of the giant sequoia.

Finally, little is known about the relationship of Douglas squirrels to forest fires. Hatt (1929) described a few of the responses, i.e. escape to tunnels and migration, of pine squirrels (*Tamiasciurus hudsonicus*) to fires in lodgepole pine forests in the Rocky Mountains of Colorado. There are few other reports, and none in the giant sequoia groves where Hartesveldt and Harvey (1967) and Hartesveldt (1964) have postulated that primeval fires were surface fires which did not often destroy the larger trees. Such fires probably had little impact on the squirrels.

The present study was undertaken to expand our knowledge of the biology of the Douglas squirrel and, specifically, to answer the following questions. What is the impact of the Douglas squirrel on the cycle of regeneration of the giant sequoia? Do Douglas squirrels consume seeds or the cones and, if so, what is their impact? Do Douglas squirrels living in giant sequoia groves behave the same and have similar ecological relationships as do those squirrels who live in non-sequoia coniferous forests? Do moderate-sized manipulations grossly affect the number of squirrels or their biology?

### Natural history

The Douglas squirrel is found in the mountainous areas of central and northern California, western Oregon and Washington and southwestern British Columbia. Its close relative, the red squirrel (*Tamiasciurus hudsonicus*) is found in the New England and Great Lakes states, the Rocky Mountain states, most Canadian provinces, and Alaska. It has been well studied (Hamilton 1939; Hatt 1929, 1943; Klugh 1927; Layne 1952; Muir 1927; C. Smith 1965, 1968, 1970), as has the Douglas squirrel in the northern part of its range (C. Smith 1965, 1968, 1970). The study of C. Smith (1968) provides us with the best account of the typical behavior of both red and Douglas squirrels throughout most of their ranges. Both species are active all year even in the most severe climates despite the fact that they are small and have very high metabolic rates (Irving et al. 1955). They are highly territorial animals which defend their territories throughout the year on an individual basis, except for a very brief period of sexual activity. Most of their territorial defense is by means of vocalizations. These are so efficient as to reduce the amount of their time actually spent defending territories to approximately 2%. C. Smith (1968) speculates that vaginal secretions of the female aide in the coordination of breeding behavior and the associated relaxation of territorial activity on the part of both sexes.

There may be one or two reproductive periods per year, depending on the habitat of the animals. Two to five young are born after a 40 day gestation period. C. Smith (1968) found that young red squirrels stayed in the nest for 50 to 57 days after birth and were not weaned until the 62nd to 64th day. He considered Douglas squirrels to have similar patterns.

Young of both species spend two to three weeks before they are completely weaned, exploring the area about their nest upon first leaving it, learning to eat adult foods, and beginning to establish territories. Their mother excludes them from her territory soon after they are weaned, and all individuals in the family group establish defended territories by the time the young are 71 to 74 days old (C. Smith 1968). The major items of food throughout most of the range of either species are the reproductive parts of conifers, deciduous trees and fungi, as well as the cambium of various bushes and pines. They typically build large nests of plant material either in trees or in the ground. The use of such nests and a diurnal pattern of activity allows them to minimize the energy spent on maintaining their body temperature. They cut large numbers of conifer cones and store the cones in caches (large numbers of cones stored in cool, dark or moist places). Such caches are easily defended and can be found and used even under the snow. Indeed, animals eating under the snow are protected from the colder temperatures above the snow level. The sizes of territories in the British Columbia populations studied by C. Smith (1968) in hemlock and in lodgepole pine forests were 0.51 hectares (1.27 acres) and 0.91 hectares (2.24 acres) respectively. The size of the territory and the potential success of its occupant surviving the winter were both related to the amount of food found in it. The function of territorial behavior in these species was described by C. Smith (1968) as ". . . to allow each individual the optimum conditions for harvesting, storing, and defending a seasonal food supply so that it will be available throughout the year. The defense of territories by single individuals allows for a more efficient storage of food than defense of territories by pairs of squirrels."

## Methods

Douglas squirrels were observed in North and Trail Areas from 1965 to 1974, Ridge Area from 1966 to 1974. The size of the observation area or plot in North and Trail Areas was 1.8 hectares (4.5 acres) each, and approximately 0.8 hectares (2 acres) for Ridge Area. The observation plots included the manipulated portion of Trail Area and most of the manipulated and control portions of North and Ridge Areas, plus a surrounding buffer zone in each case. The zone of observation was enlarged to 30 hectares (75 acres) in each area in 1974 because of the extremely low and widely dispersed population of squirrels at that time.

Douglas squirrels were censused using the plot census method developed for birds by Kendeigh (1949). Dittoed maps of each area of observation were used, on which to record each day's observation. Eight-power binoculars were used for observations. Field records were kept and correlated with the results of the plot censuses. No attempts were made in the early part of the study to capture and mark animals due to the distances

involved in observing them and their wariness of the traps. Observations were made one to two times a week in July and August of 1965, 1966, 1967, and 1974; six days in August and September in 1968; seven days in 1969; four days in 1970, 1971, 1972, and 1973; one day checks in May and October from 1965 to 1968; and one day in October in 1970, 1972, 1973, and 1974 for a total of approximately 650 hours of observation.

Estimation of cone loads on giant sequoias was difficult because the cones remain green and unopened for many years and because each large tree bears a great number of relatively small cones. Cone loads were estimated from the ground for nineteen randomly selected trees in the various areas during 1967 and 1968 using eight-power binoculars. Cone categories used were: 1 = load consisting almost entirely of a few terminal cones; 2 = some concentrations of cones (10–50), few terminal cones or, in some trees, the terminal cones comprising the bulk of the cone load; 3 = few major bundles of cones and then only 20–60 cones per bundle; 4 = numerous large groups of cones (60–200) found on most, or at least a majority of branches with a moderately heavy terminal cone load; and 5 = very heavy load of cones, many large groups of cones with most to all exterior branches filled with cones and with a heavy load of terminal green cones. First year (or new cones) are of a different hue of green than older cones, and their numbers were also estimated on each of the nineteen trees. The cones in one of these trees (the Castro Tree in South Area) were counted from within the tree a year later by Stecker (Chapter 7) and a count for the year in question was calculated by subtracting the numbers of first year cones from that exact count. A cone load factor for that tree was obtained by multiplying the estimated cone load of the tree times its dbh. The number of cones on the same tree was divided by the cone load factor to obtain a multiplier figure which could be multiplied by the cone load factors of other trees to obtain an estimate of the number of cones for each of them.

Early observations during the course of the study revealed that individual giant sequoias were never inhabited by more than one squirrel during any one year. Hence the number of cones cut and chewed per unit time could be estimated by clearing cones from beneath occupied trees in the fall of one year, and picking up and counting the newly cut cones in the next summer. This was done for four trees.

Time spent by cones on the ground was visually estimated by comparing changes in them to the changes that took place in cones previously monitored for known periods of time. Recently cut and chewed cones were yellowish-green, while those down for a few months were rusty brown, and year old cones were grey-brown.

The potential use of sequoia seeds by squirrels and other mammals was checked using the seed spot technique described in Chapter 8.

The potential impact of the squirrels on seeds in cones was checked

by shaking out the remaining seeds from 100 chewed and partially dried cones randomly collected in the study areas, and from inspecting 1383 seeds taken from eating places. The viability of these seeds was checked using a snap test.

Potential age-class preference for cones by the squirrels was assessed by comparing 250 green cones removed from six branches of a study tree in South Area with 160 fresh green cones cut by Douglas squirrels from four other trees in the study areas. The age of cones was established by using a dissecting microscope to aid in counting the rings of their peduncles.

The caloric value of giant sequoia seeds and cones was established by burning four samples of seeds and the outer portions of three cones in a standard oxygen bomb calorimeter. Rough estimations of the portions of the cones eaten by squirrels were made by trimming unchewed cones to the approximate configurations of chewed cones. All samples were oven dried to a constant weight at 65–70°C. No additives were needed to insure combustion, as preliminary tests resulted in almost total combustion.

## Results

### Numbers and densities

The number of Douglas squirrels fully or partially inhabiting the 4.4 hectares in Ridge, North and Trail Areas ranged from a high of 36 animals in the late summer of 1966 to 1 in 1974 (Table 24). The population had decreased to such a low level in 1974 that the area of observation was increased to 90 hectares in which there were eight animals. The aggregate number of territories varied from a high of 11 territories per hectare in Trail Area in 1966 to zero in 1974 (Table 24). The average density likewise ranged from a high of 6.4 squirrels per hectare in 1966 to 0.09 squirrels per hectare in 1974 (Table 24, Fig. 61).

The minimum size territory was approximately 0.28 hectares (0.69 acres) and was reached in 1966. This space was the smallest in which both a large giant sequoia and a large white fir could be found, and both appeared to be necessary for a successful territory (Table 25). The numbers of animals dropped to very low levels in 1973 and 1974 during which time territorial defense and stable territories nearly disappeared. Animals wandered over one to two hectare zones with seven to fifteen hectare neutral zones surrounding them.

The average distance between centers of activity varied greatly during the years of the study (Table 25). Average distances in the range of 40 to 60 meters, as in 1966 (Table 25), were associated with intense territorial interactions. Animals with territories centered 150 meters or more apart, or whose territories were much larger than 1 hectare (Table 25), exhibited little territorial behavior towards each other.

**Table 24.** Numbers and densities of Douglas squirrels.

Year	Ridge Area (0.8 ha)		North Area (1.8 ha)		Trail Area (1.8 ha)		All Areas	
	No. animals	No. territories <sup>a</sup>	No. animals	No. territories	No. animals	No. territories	density per acre	density per hectare
1965	—	—	6	6.0	8	7.5	1.5	3.7
1966	12	7.5	12	10.0	12	11.0	2.6	6.4
1967	1	1.0	1	1.0	5	4.5	0.6	1.5
1968	3	3.0	4	2.0	4	3.5	0.8	2.0
1969	2	1.5	2	1.5	4	3.5	0.6	1.5
1970	3	2.0	7	6.5	5	4.0	1.1	2.7
1971	2	1.0	4	4.0	3	2.0	0.6	1.5
1972	3	1.5	4	3.0	3	1.8	0.6	1.5
1973	2	0.8	2	1.0	2	0.5	0.2	0.5
1974	0	0.0	1	0.5	0	0.0	—	—
1974 <sup>b</sup>	4	4.0	2	2.0	2	2.0	0.04	0.09

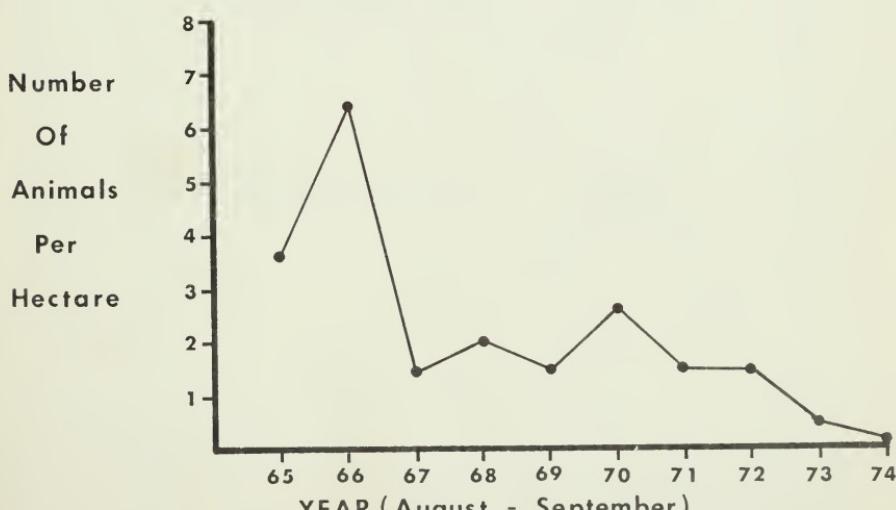
<sup>a</sup>Total of full and partial territories<sup>b</sup>Each area studied enlarged to 30 hectares (75 acres) in 1974**Fig. 61.** Mean densities of Douglas squirrels in Ridge, North and Trail Areas (based on August-September data).

Table 25. Average size of territory or area occupied and average distance between centers of activities of Douglas squirrels.

Year	Ridge Area		North Area		South Area		Mean size territory (hectares)	
	Territory in hectares	Distance between centers in meters	Distance between centers in meters		Territory in hectares	Distance between centers in meters		
			Distance between centers in meters	Territory in hectares				
1965	—	—	0.69	124	0.42	75	0.52	
1966	0.28	40	0.32	61	0.28	66	0.28	
1967	0.66	102	0.68	243	0.67	66	0.66	
1968	0.48	54	1.26	78	1.01	65	0.82	
1969	0.68	161	0.51	192	0.66	152	0.62	
1970	0.40	151	0.64	82	0.49	66	0.52	
1971	0.68	215	0.70	90	1.10	140	0.76	
1972	0.40	91	1.14	80	0.83	103	0.74	
1973 <sup>a</sup>	9.12	200	5.47	155	5.47	210	6.31	
1974 <sup>a</sup>	7.50	1500	15.00	1100	15.00	11.80	11.38	

<sup>a</sup>Territories of 1 to 2 hectares were established inside these larger areas.

## Natural history

No large nests of plant materials, so characteristic throughout most of the squirrel's range, were found in any area of giant sequoias in the ten years of the study. Stecker found a possible nest at an elevation of 82 meters (270 ft) in his study tree in South Area in 1970. It was a hole 20 × 36 cm and contained numerous fecal pellets of Douglas squirrels, some shredded bark and some old pine seeds. It is not known whether this was a summer or winter nest, or both. Numerous growths in old white firs were observed carefully from the ground and none of them appeared to be any kind of nest. The occasional holes in the trunks of giant sequoias, other than the two climbed and examined by Stecker (Chapters 6 and 7), could not be examined due to the difficulty in climbing such trees.

Douglas squirrels apparently used shredded bark to line their nests. Suppressed giant sequoias with their lower trunks shredded are common wherever Douglas squirrels have resided for any length of time. George Lawrence (pers. comm.) suggested that both Douglas squirrels and grey squirrels (*Sciurus griesus*) shred giant sequoia bark for bedding material. Most of the shredding activity was attributed to Douglas squirrels as most of the affected trees were in or near known territories and because the grey squirrel population was far smaller. The only sighting of animals actually shredding young sequoias was by Karen Shellhammer (pers. comm.), and that was of a Douglas squirrel shredding a small tree among a group of previously shredded trees. Trees used for shredding were always small (10–20 m tall), suppressed and growing in dense groups. A few to most of the trees in such a group were shredded over 50 to 80% of their diameters and from 10 cm to 8 m off the ground. They were stripped of their bark but not their cambium and were still living. Occasionally one of the smallest trees had enough cambium removed so as to kill it.

Precise data concerning reproductive rates and longevity were difficult to collect as the animals were not marked. It was possible, however, to gain a general idea of these patterns because many of the animals maintained stable territories for several years, especially in years of moderate to high densities. The mean life span of these animals was estimated to be approximately two years, although this figure is influenced greatly by the high mortality in 1966–67 when 30 of 36 animals apparently perished.

Second litters were seen outside the study areas in 1965, 1966, 1969, and 1972, and in summers following mild winters and early growing seasons. Douglas squirrels are not weaned until 102 to 104 days following conception (C. Smith 1968) and usually established territories in late July and August. Second breedings apparently did not occur in the study areas in any year and were infrequent in the Redwood Mountain area. No accurate measurement is possible for the average number of young produced per year.

## Foods

The major item in the diet of Douglas squirrels in the study areas was the cones of giant sequoias. They were taken nearly year round in years when the squirrels were dense and primarily in the fall, winter and late summer in other years. The squirrels switched to white fir, sugar pine and/or ponderosa pine cones as they matured in the last part of August or early September each year. The cone type consumed depended upon the relative abundance of its cones during the fall. White fir cones were extremely abundant and used heavily in 1973 but were absent altogether in 1974. The few squirrels that were present in 1974 turned to ponderosa pine, as the sugar pine crop was also poor and patchy in distribution. The squirrels usually spent two weeks feeding on these alternative conifer cones but never were seen to cache them. Douglas squirrels cached only giant sequoia cones in the study areas, whereas they cached the cones of other species of conifers in nearby nonsequoian forests. This phenomenon represents a primary departure from Douglas squirrel behavior in the rest of their range.

Douglas squirrels harvested hazelnut (*Corylus rostrata*) and mountain alder fruits (*Alnus tenuifolia*), the latter to an undetermined degree, each August and September. Fungi of a variety of species were eaten throughout the summer and early fall and some were stored for winter use.

Those Douglas squirrels observed eating giant sequoia cones took about 15 to 30 minutes to chew away the outer portion of the cone. They were never observed to eat brown, dried cones or those with several to many brown scales on them. Squirrels were observed eating cones while at the base of a tree or on branches 3 to 10 m above the ground. Those eating cones in the upper branches of 85–100 m tall giant sequoias were unobservable. Cones were picked up with both forefeet, with one end held higher than the other. The cone was rotated with the forepaws as the outer portion of each green scale was chewed off and dropped. The tips of several scales were trimmed before the squirrel concentrated on individual scales. The upper and lower surfaces of each scale were scraped repeatedly before the animal switched to the next scale. Some of the seeds attached at the base of the scale were consumed in this process, but most of the six to eight seeds attached to each scale remained attached and undamaged or were spilled from the cone in a relatively undamaged condition along with some of the scrapings from the scale. The pattern of rotate, trim and chew was continued until most of the scales of the cone had been worked, and then the cone was dropped. Some squirrels had "signatures" in relation to the amount of green cone they left uneaten (i.e. one ring of scales, two, three, etc.) (Fig. 62). A small percentage of squirrels stripped the cone almost to the main axis leaving an object resembling the core of a small, well-eaten apple. Squirrels groomed their faces with their hindfeet and cleaned their whiskers by rubbing their faces on a branch of a tree.

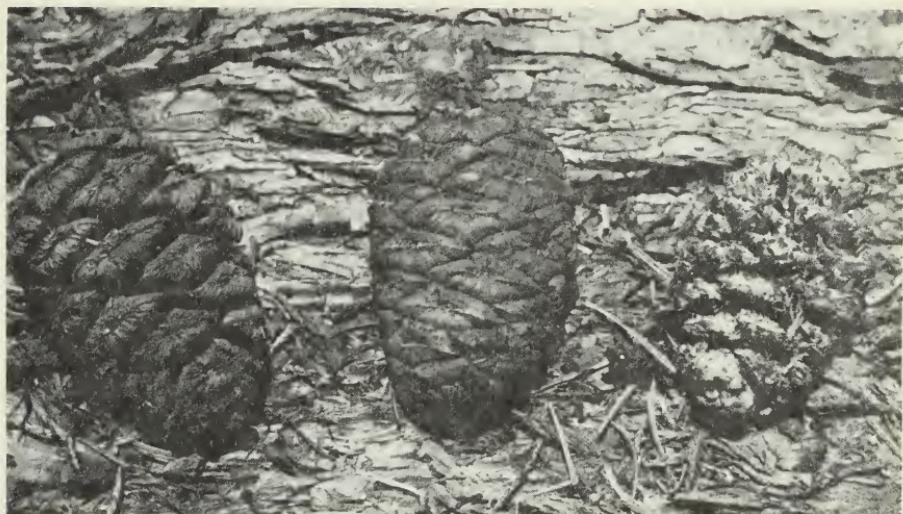


Fig. 62. *Sequoia* cones: dry, brown cone on left; green, fleshy cone in center; cone chewed by Douglas squirrel on right.

Chewed and partially dried cones picked up from the ground were found to have a small percentage of their seeds, and most of these were relatively undamaged physically. Two hundred and nine seeds (67%) of 310 shaken from 100 dried cones were whole and undamaged. Thirty-eight percent (525 of 1383) of the seeds collected from an eating place, or "kitchen midden," were whole, whereas 62% were physically damaged, although most of the damage was to the sterile wings of the seeds. The viability of such seeds was reasonably high (29%) using a snap test. This level of viability compares favorably with the results of controlled drying tests of seeds and indicates that the saliva of the squirrels does not appear to damage the seeds.

### Cone cutting behavior

Douglas squirrels used three different patterns of cutting giant sequoia cones. They cut large numbers of cones in a short time, small numbers intermittently over a long time, or they cut individual cones and ate them. The most dramatic of these was the cutting of large numbers of cones in brief periods of time. Shellhammer's report (1966) of one squirrel's cutting 538 cones from one tree in 30 minutes is the most stunning example of this pattern. The squirrels cut rapidly and yet selected for certain age classes of green cones and excluded brown and nearly all partially brown cones. Cones cut in such periods were cached in several ways. Some animals buried 2 to 5 cones in little pits dug in the ground within ten

meters of the base of a giant sequoia or about its base where the duff was especially thick. Other animals cached cones in the dark, cool, deeper parts of fire scars. The fire scar of one giant sequoia contained 538 cones in one scar and 189 in another. The caching of 500 to 750 cones, regardless of the type of cache, usually required three to four days. A third type of cache was found in damp or moist areas. One such cache in Trail Area in 1966 contained an estimated 725 cones in three groups along a seasonally moist area. There are numerous reports of similar types of caches of other conifer cones in nonsequoian forests. Shaw (1936) reported on the caching activities of various subspecies of Douglas squirrels and noted that such cool, moist places were extremely effective in keeping cones green and moist. Douglas squirrels, however, do not cache their cones in creeks. Cones end up in water courses by accident when squirrels cut trees near them. Cones are cut from the upper regions of giant sequoia trees and fall in 180° to 360° arcs about their bases. The squirrels subsequently place those cones that have fallen onto the forest floor in caches. They do not attempt to retrieve cones from creeks, and the currents tend to deposit cones in low spots, hence the appearance of "aquatic caches."

A second pattern of cone cutting occurred at much lower levels of intensity. Cones were cut in small numbers per period of cutting over longer periods of time, and each group was eaten or cached before another group was cut. Cones were cached poorly or, often, not cached at all when the numbers of squirrels were low. New cones were cut when the last few cones of the group cut previously began to dry out and were no longer edible.

The third pattern was one in which squirrels cut, ate and dropped individual cones from the tree itself. This pattern was quite variable, being exhibited by many young squirrels and by many adults during fall and winter. The numbers of adults exhibiting the last two low intensity patterns increased in years when the populations of squirrels were low.

The patterns of cone cutting and territorial behavior will be discussed as they appeared in years of high, moderate to low and very low numbers of squirrels.

### Behavior in years of high densities

The summer of 1966 produced the highest densities of Douglas squirrels observed during the length of the study (Table 24, Fig. 61). Territorial activity was intense, with the highest frequency of vocalization per animal demonstrated. Many chases took place, and several of the chases observed in August ended in physical contact and cries of pain on the part of the bitten animals. Alarm calls directed towards the investigators were easily elicited and at greater distances than in any other year.

Squirrels were nearly equidistant from one another, with a giant sequoia as the center of each territory. Each territory contained one or more large,

old white firs which often served as access to the big tree. Squirrels restricted their cone-cutting activities to a single sequoia, even in territories where two or more sequoias were present. Cones were cut in great numbers. In addition to the bout described by Shellhammer (1966), individual squirrels were observed to cut 650 cones in 55 minutes, 206 in 17 minutes, 290 in 3 hours, and 997 in 5 ½ hours. Another animal cut 1,430 cones in three bursts of several hours spread over a three-week period. Almost all cones cut were cached about the bases of giant sequoias or in wet areas. Most of the cones cut were eaten on the ground, at kitchen middens, or on the lower branches of trees.

Douglas squirrels were intolerant of other species of rodents, especially chipmunks (*Eutamias* spp.). Chipmunks were chased from caches of cones, while California ground squirrels (*Otospermophilus beecheyii*) were threatened but not attacked by the Douglas squirrels.

### Behavior in years of moderate to low densities

The summer of 1968 followed the second driest and mildest winter of the period of the study. The numbers and densities of Douglas squirrels were approximately one-third that of 1966 (Table 24, Fig. 61), and the size of their territories was approximately three times greater (Table 25). Territories included five or more giant sequoias, and two or more of them were cut by most squirrels during the year. All types of calls were low in number and most animals gave fewer territorial calls than in 1966. Juveniles had much larger unoccupied and undefended spaces between existing adult territories into which they could move to set up their own territories. Adults actively defended a central core of 0.7 to 1.0 hectares about the tree or trees in which they were residing and weakly defended a narrow buffer zone around the core.

Few squirrels cached large numbers of cones. One squirrel cached 350 cones in an old, downed sequoia, but this animal exhibited similar behavior each year, unlike most other squirrels. Several animals cut a majority of first year cones, although this was the only year of the study that it occurred to any extent. Animals cutting 30 cones or more at one time seldom cut any first year cones. No long bouts of cone cutting were observed, nor were any large caches of cones found.

Sugar pine and white fir cones were used heavily in late August and September, as they were in 1966.

### Behavior in years of very low densities

The populations of Douglas squirrels were about 70 times lower in the summer of 1974 than they were in the peak year of 1966 (Table 24, Fig. 61). The population had dropped to the second lowest level during the period of the study in 1973 following a very severe winter. The winter of 1973–1974 was average for the period of the study but was followed by

an even further drop in the numbers of squirrels. Only one animal was found in any of the study areas in the summer of 1974, hence the decision was made to enlarge each area of observation to 30 hectares (75 acres). Eight animals resided in the 90 hectares comprising the new study areas.

Calling nearly disappeared throughout the summer, with the exception of a few territorial calls in August. Animals did not give alarm calls to the presence of investigators unless they were surprised at close distances. Only one of the eight animals cut cones in any numbers: cutting an average of 200 cones a day in late August. It was also the most vocal animal.

Territories were essentially nonexistent as the center of activities were 1100 to 1500 meters apart (Table 25). No single giant sequoia was used for more than several weeks to a month with the exception of the animal described previously, and that animal became established only after residing in three other sequoias for brief periods of time. The average squirrel used seven trees from the winter of 1973 to late August in 1974. Most cones were cut and eaten singularly in the upper parts of the trees and then dropped. Each of the squirrels, however, cut 150 or more cones a day on three or four days in July or August. These were not effectively cached and in several cases not even eaten. Some cones were superficially cached on the top and along the sides of downed trees, and no large caches were found, with one exception. Almost all of the cones in these occasional bouts of cutting dried out on the ground and became inedible. The general pattern was for an animal to eat cones in a tree for several weeks, cut a number of cones, eat a few of them and then move on to another giant sequoia 20 to 200 meters away.

The white fir cone crop failed and there were few sugar pine cones. Occasional sugar pine cones were eaten early in the summer, an unusual activity when compared to other years.

### Age class preference for cones by squirrels

Most (84.9%) of the cones cut by Douglas squirrels were in the 2 to 5 year age classes, while only 46.3% of the cones taken from the study tree were of those age classes (Table 26). The squirrels took very few older cones, as was the case with almost every group of cut cones examined throughout the study.

### Impact of Douglas squirrels on cone loads

The giant sequoia used as a reference point (Castro Tree in South Area) was estimated to contain approximately 18,000 cones in 1969 based on a count made from within the tree by Stecker and Shellhammer. A more accurate figure of 18,411 (for 1969 cone crop) was obtained in 1970 by subtracting the number of first year cones (20,697) from a cone by cone count of the tree (39,508) done by Stecker in that year (Chapter 7). The estimated number of cones in the Castro Tree (18,411) was divided by its

**Table 26.** Age class distribution of giant sequoia cones versus age class preference by Douglas squirrels.<sup>a</sup>

Age class of cones in years	Percentage of 160 cones cut by squirrels	Percentage of 250 cones from Tree 15, South Area
1	3.8	16.0
2	23.1	5.2
3	38.8	19.5
4	15.0	15.6
5	10.0	10.0
6	5.0	5.0
7	3.1	10.0
8	—	5.2
9	—	2.4
10	0.6	4.8
over 10	0.6	7.2

<sup>a</sup>A chi-square test showed the differences to be highly significant ( $p < .001$ );  $\chi^2 = 116.3$ , d.f. = 10.

cone load factor (44) to yield a multiplier figure (418.43). This figure was multiplied by the cone load factor of each of the other trees in the sample to obtain a rough estimate of the numbers of cones in each of them. Using this method the average number of cones on 19 trees was 14,117 (5,021 to 25,106). The numbers of cones on large giant sequoias on Redwood Mountain varied from a few hundred to an estimated 55,000 or more. Stecker's (Chapter 7) as well as my own estimates indicate that 60 to 66% of the cones on an average tree are green and 33–40% are brown at any particular time, except after such exceptional years like that in 1969–70 when great numbers of first year cones were produced. Approximately 16% of the green cones are first year cones (Table 26), although a much higher percentage can be present following favorable wet years (Chapter 7). Using these figures, the number of green cones on an average giant sequoia in the study areas was estimated to be approximately 9,000, of which 1,500 are added each year, and a similar number was expected to turn brown or be knocked off by snow or wind.

To get an idea of the magnitude of the number of cones produced in the four study areas during the ten years of the study, one can consider the cone loads estimated in 1967 and 1968 as a starting point, and that 16% of that green cone load would be added per year for a very conservative figure. The estimated starting load of green cones on the 65

largest giant sequoias in and near Ridge, North and Trail Areas was 578,110, plus 92,495 added for each of nine years, for an estimated ten year total of 924,950 cones. This works out to about 9,000 cones/ha/yr being produced. If a steady state of cone production existed, seed production would be about 1,800,000/ha/year.

Most (86.6%) of the 65 largest giant sequoias in the study areas had cones cut from them by Douglas squirrels during the ten years of the study (Table 27). Cones from two trees were cut in nine of the ten years, but relatively lightly in the last three of those years. Eighteen trees were cone-cut heavily (2,000 cones/year or more) from one to six years (Table 27). Each tree was estimated as being lightly cut (1 to 100 cones, average of 50), moderately cut (100 to 1,000, average 500) or heavily cut (1,000 to 3,000+, average of 2,000). An estimated 135,505 cones were cut from the 65 trees in the ten years, or 2,085 cones per tree in ten years. This is an average of 209 cones per tree per year, but this figure rises to 251 cones per tree per year if uncut trees are excluded.

Coefficients of correlation between cone load (as of 1967-68) and the number of cones cut in the ten year period for Ridge, North and Trail Areas were 0.40, -0.36 and -0.25 respectively. Hence there was no obvious tendency by squirrels to select trees with high cone loads. Only six trees had 10,000 or more cones cut from them during the period of the study. Two of these trees had light cone loads (5,000 and 7,000), two were in the third heaviest category (of five) and two were in the second heaviest category. One tree was used for seven years in a row; another for six years. Most trees that were used heavily were cut in two series of years with several years of disuse in between. A somewhat random alternation of tree use was produced by a combination of: young squirrels establishing territories in the free spaces between existing adult territories; the creation of free spaces between the young squirrels' territories by the subsequent deaths of the adults; fluctuations in the size of territories; and the number of trees used within each territory. Few trees were used repeatedly for long periods of time because of these factors.

### Caloric studies of cones and seeds

The mean caloric value of giant sequoia seeds as measured by bomb calorimetry was 4,738 cal per gram d.w. and that of the outer portions of the cones was 4,690 cal gram d.w.. The outer portions of four cones (mean weight = 59.3 g) were trimmed to approximate chewed cones. The trimmings averaged 33% (19.7 g) of the wet weight of the cone and were dried to an average of 10.2 grams. Using C. Smith's calculations (1968) as a model, 9.5 grams of what was lost were considered to be water or plant juices and 1.2 grams of the dried trimmings were estimated to be indigestible supportive materials, leaving 9.0 grams, or 15% of the total wet weight, of each cone as dry weight material available to a squirrel.

**Table 27.** Giant sequoias in which Douglas squirrels cut cones.

Number of years	Trees cut at any level of activity <sup>a</sup>		Trees cut heavily; 2,000 cones or more	
	Number of trees	Percentage	Number of trees	Percentage
0	10	15.38	47	70.76
1	18	27.68	6	9.32
2	10	15.39	2	3.08
3	10	15.39	4	7.69
4	5	7.69	3	4.62
5	2	3.08	2	3.08
6	2	3.08	1	1.54
7	4	6.15	—	—
8	2	3.08	—	—
9	2	3.08	—	—
Totals	65	100.00%	65	100.00%

<sup>a</sup>From 50 cones or more per year to more than 2,000 cones per year.

Net energy available to a squirrel also was estimated using the guidelines of C. Smith (1968) for both Douglas and red squirrels. He suggested they digest a high percentage of their food and that the calorigenic effect of assimilating it was low. He used a figure of 75% of the ingested food energy as an estimate of net energy, while 70% is used in this study, as the author estimates the squirrels are ingesting more crude fiber. Measurements of 65 cones from various areas yielded an average weight of 46.2 grams. The maximum energy gained from eating such a cone is calculated as  $46.2 \text{ g} \times 0.15 (\% \text{ dry wt [d. w.] of chewed materials}) \times 0.7 (\% \text{ of ingested material assimilated}) \times 4,690 \text{ cal per gram d.w.} = 22.8 \text{ kg calories per cone}$ . This figure is a liberal one; most animals likely eat less of the cone than the estimated trimmings as they discard the tips of the scales and spill some other tissues. A squirrel eating such a cone in 20 to 30 minutes could obtain 1.14 to 0.76 kg cal per minute, whereas the energy obtainable from the average of 200 seeds for such a cone is far lower. Two hundred seeds in an average cone yield 1.4 kg cal, or from 0.07 to 0.05 kg cal per minute over 20 to 30 minutes. Hence a Douglas squirrel might gain 10% more food energy and a possibly more nutritious

food by eating all the seeds of a green sequoia cone in addition to the outer portions of the cone, but very little energy (0.05 to 0.07 kg cal per minute) if it tore a cone apart solely to obtain the seeds. The latter intent would provide about one-fifteenth the energy gained by eating the scales, assuming that both or either activity took an average of twenty minutes.

Douglas squirrels cut 2,719 and 3,750 cones from two different giant sequoias in 318 days during 1968 and 1969 for an average of 8.6 and 11.8 cones per day. These figures are a bit misleading as it is probable that fewer cones were eaten in some months when other conifer cones and fungi were available. More cones were eaten most likely in late winter and early spring when all other food sources were used up. Squirrels also removed 2,082 and 1,583 cones from other marked trees during 1971 and 1972, but the number of days could not be determined. It is estimated, using these figures, that a squirrel might cut and eat on 2,500 to 4,500 giant sequoia cones per year in addition to much smaller numbers of white fir or sugar pine cones plus fungi and assorted other foods.

### Weather factors

Measurements of temperature and snowfall taken from Grant Grove approximately 300 meters higher and 5.5 kilometers away from the field areas showed a winter average maxima 5°C colder and average minima 3°C higher than in the study areas, while summer average maxima and minima were the same. Two measures each of heating degree days and snowfall are shown on Table 28. Heating degree day measurements are standard U.S. Weather Bureau figures for a number of degrees (in °F) below 68°F each day on a monthly basis. Sixty-eight degrees F is also the critical temperature below which the Douglas squirrel has to expend in excess of basal metabolic requirements to maintain a constant body temperature (Irving et al. 1955). Irving et al. (1955) determined the figure for animals belonging to a subspecies of red squirrel in Alaska, but both C. Smith (1968) and the present investigator consider it to be similar in Douglas squirrels. The relationship between the average density of the squirrels in Ridge, North and Trail Area (from Table 24) and number of heating degree days both per year and in the colder period from January through June each year can be seen on Table 28. The coefficients of correlation in comparing squirrel densities and the two measures of temperature were -0.53 and -0.59 respectively. The correlation coefficient between total snowfall per year and density was much lower, at -0.34, although there was a stronger relationship between the lateness of the snow and a drop in the density of the squirrels. The numbers of squirrels decreased from the level of the preceding summer in 1967, 1969, 1971, and 1973 when the snows were heavy and late. The snow was very late on the ground in the spring of 1967 when 363 cm of 681 cm total snowfall (143 of 268 in) fell in April. The winter of 1970-71 was average for the

Table 28. A summary of weather factors and changes in densities of Douglas squirrels.

Year	Avg. density of squirrels per hectare <sup>a</sup>	Compared to the previous summer	Heating degree days per year <sup>b</sup>	Heating degree days, Jan.-June	Compared to previous year	Total snow per year cm (in)	Month(s) of heaviest snowfall
1964-1965	3.7			7104	4482	602(237)	April
1965-1966	6.4	more		6601	3955	559(142)	December
1966-1967	1.5	less		7021	4598	681(268)	April
1967-1968	2.0	more		6390	4074	292(115)	December
1968-1969	1.5	less		7237	4520	856(337)	February
1969-1970	2.7	more		6619	4231	272(107)	March
1970-1971	1.5	less		6874	4381	518(518)	December
1971-1972	1.5	no change		6741	3805	391(145)	December
1972-1973	0.5	less		7537	4469	765(301)	Oct.-Feb.
1973-1974	0.09	less		6827	4194	498(196)	Jan.-March
Average				6895	4271	521(205)	

<sup>a</sup>From Table 24 for the summer of the second year listed.<sup>b</sup>Weather data from Grant Grove, Kings Canyon National Park. Heating degree days = number of degrees (in °F) below 68°F each day during a particular period of time.

period of study, but the snow was distributed more or less equally when 29 cm of 518 cm (11.6 of 203.6 in) fell as late as May. Decreases in numbers of squirrels therefore appeared to be correlated with a variable combination of winter temperature, total snowfall and the lateness of the snow-pack (and associated lower than usual temperatures).

### Responses of squirrels to manipulations

Planned surface fires, litter removal and pile burning on plots of 1 to 2 hectares did not appear to have any effect on the numbers of Douglas squirrels. No major differences in numbers were seen between the treated and control areas in Ridge, North or Trail Area following treatment. Douglas squirrels apparently were unaffected by larger prescribed burns carried out on Redwood Mountain in 1969. Douglas squirrels were observed to move across the manipulated area soon after the ashes cooled, and cone cutting commenced several days after the fires. The survival of these animals over a longer period of time was not studied to the extent of those in our study areas, hence the long term effects of large scale manipulations could not be assessed.

### *Discussion*

The most obvious difference between Douglas squirrels living in giant sequoia forests and those inhabiting other types of forest is that they store giant sequoia cones to the exclusion of all other species of conifers. They eat the seeds of other conifers when they are available but they do not cache any of them. The range of foods eaten, other than conifers, is otherwise quite similar in scope to that reported by C. Smith (1968) in British Columbia, although sequoian squirrels do not appear to store hazelnuts or fruits of mountain alders.

No large tree nests were observed in a giant sequoia forest during the period of the study. Douglas and red squirrels are known to nest in hollow trees, hollow logs, outside tree nests of grass or foliose lichens, or holes in the ground (C. Smith 1968). Their nesting material may include grass, shredded bark or lichens; circumstantial evidence indicated that sequoian squirrels used considerable amounts of shredded sequoia bark. No large ground nests were discovered, and the one tree nest discovered by Stecker (pers. comm.) in the upper part of a giant sequoia offered its occupant little protection from weather and predators.

Large numbers of sequoia cones were stored and eaten at caches in years of high squirrel densities. Most cones were eaten in the trees in winters when the numbers of squirrels were low. This must have exposed the animals to lower winter temperatures for longer periods of time than C. Smith (1968) suggested was the case in British Columbia. He suggested they spent much of their time in their tree nests or beneath the snow

eating cones stored there in large caches. Michael Smith (1968) reported that the Alaskan red squirrels also spent much of their time beneath the snow, eating and resting during the coldest periods of the winter.

There was no major movement of squirrels from one area to another. Such movements have been reported for Douglas squirrels from other regions, where they moved from areas of low to those areas of high food availability (Merriam 1884; Klugh 1927; McKeever 1961; C. Smith 1968).

Sequoian squirrels generally had one litter per year with a few exceptions in the drier, warmer years. C. Smith (1968) noted that Douglas squirrels in the Pacific Northwest west of the Cascades generally had two breeding seasons. There the group of young produced by later winter matings were fed on cached cones, while those of late spring matings were fed on the new season's cones.

Sequoian Douglas squirrels did act quite differently than those from nonsequoian forests. No animals were studied along the edge between a dense grove and a more diverse Transition or Canadian Zone forest to see if their preoccupation with giant sequoia cones remained. This species is quite adaptive behaviorally, and many of the patterns observed in this study must have been shaped by imprinting and other early learning of the young squirrels.

### Territoriality

The territorial behavior of sequoian Douglas squirrels is different than that of squirrels living in other forests, especially in more northerly ones. The territories reported by C. Smith (1968) were centered about a group of cone-producing trees and one to several caches. Kemp and Keith (1970) reported that the closely related red squirrel in New York state had two types of territories. One was a prime territory, which was similar to that described by C. Smith (1968) in that it contained a group of conifers producing a good supply of seed and was defended all year. The second type of territory was the winter food cache, which was defended only in the winter. These territories are all centered about a seasonal food supply. C. Smith (1968) defined the function of territorial behavior as allowing "each individual the optimum conditions for harvesting, storing, and defending a seasonal food supply so that it will be available throughout the year." Brown (1964) suggested that some resources are distributed in time and space so as to be economically defensible, and conifer cones certainly are one such resource. The dispersion of most Douglas and red squirrels appears to be a combination of a reasonably uniform distribution of food and of the agonistic behavior of the squirrels themselves. Agonistic behavior is described here as a collective term for attack, threatening, retreat, and/or submissive behaviors. Douglas squirrels usually have low enough densities that their highly aggressive behavior causes them to be dispersed in a more or less regular pattern. High densities may force some squirrels

into less suitable habitat (Brown and Orians 1970), and in nonsequoian forests this may end in the death of the individual (C. Smith 1968). Agonistic behavior continues to play a very important role in giant sequoia forests even though the food supply is, for all intents, a constant one.

The animals in the present study were quite regularly spaced at all population densities except the very lowest levels. Such a regular pattern of dispersion is quite important as it tends to minimize the number of possible competitors about any particular animal. This type of territorial defense is optimal where the numbers of individuals are moderately low and a food resource is stored in the center core of a territory (Hamilton and Watt 1970). Such territories become less efficient with two animals in them as the maximum radius will have to be doubled to provide food for the two animals. The total locomotive effort required to obtain all the resources in such a territory will increase by the same amount (C. Smith 1968). Individual territories are most efficiently maintained if their perimeters do not have to be patrolled by the occupant. Douglas squirrels use vocalizations directed from the core of their territories for most of their territorial defense. C. Smith (1968) noted that 76% of their defense was vocal, and only 24% involved chasing intruders. The squirrels he studied were so efficient as to spend but 1 to 2% of their time defending territories.

The territories in giant sequoia forests served as something more than a food source to Douglas squirrels in years when their numbers were high. A giant sequoia, which always had more than one year's supply of cones on it, became the focal point of an animal's agonistic behavior in keeping other squirrels a certain distance away from it. The density never reached the point where each large sequoia was inhabited by more than one squirrel, and it is questionable whether such a situation could occur. The large sequoia approaches being a supernormal stimulus for aggressive behavior in these animals, as well as the center of a territory.

The behavior of these squirrels at low densities is equally intriguing. Territorial behavior essentially disappears when animals are separated by more than 200 to 300 meters. The use of one sequoia becomes infrequent and animals move between sequoia trees. They cut most of their cones in the trees and must increase their exposure to lower winter temperatures, in contrast to the situation at high densities where they apparently eat at caches. Such behaviors would appear to decrease the chances of survival of an animal in years of low population densities.

### Impact of Douglas squirrels on giant sequoias

Douglas squirrels have a moderate to slight impact on giant sequoias. Most trees in a hectare are cone-cut in any ten-year period but few trees are cut heavily. An occasional tree with a light cone load may become the core tree of a long-lived female and may have most of its cones removed from it for five to six years, but such a situation is rare. Such

trees are seldom used by two generations of squirrels and hence have a good chance of producing new loads of cones, and in a few years will be up to average for cone load.

The cutting of giant sequoia cones is nearly a year-round activity and as such may aid in the regeneration of the grove. Most of the seeds dropped either from the trees or on the ground are relatively undamaged, although those seeds dropped during the summer almost certainly die because of desiccation (Chapter 5) or arthropod damage (Chapter 7). Those seeds dropped just before the first snow or just as the snow melts may contribute to sequoia regeneration, assuming other conditions are near optimum. The rate of success of sequoia regeneration due to the activities of Douglas squirrels must be extremely low, but it is partially balanced by the very slow rate of replacement of the tree.

### Impact of manipulations on Douglas squirrels

The numbers and behavior of Douglas squirrels do not appear to be affected by treatments of the type and size described in this study. Little inference can be made as to the potential effects on them of large scale managed fires.

### Sequoia cones, weather, and the survival of Douglas squirrels

Douglas squirrels are extremely active animals, both behaviorally and metabolically. Applying the figure of Irving et al. (1955) for the Alaskan red squirrel to Douglas squirrels, they have 1.76 times the basal metabolic rate expected from the relationship between weight and metabolic rate for most animals. If this rate was applied to Douglas squirrels, a male would have enough energy to perform heavy labor 24 hours a day or to put on several grams of weight a day. A female could work as hard and still supply adequate food for her young. C. Smith found that adult squirrels of 243 to 289 grams ingested between 109.7 and 322.3 kcal/day during the summer months. He calculated the daily energy requirements for the colder half of the year to be two-thirds that of the summer period because squirrels in his area readily ate stored materials from large caches and spent most of the rest of the time in their nests. The squirrels in sequoia groves are more likely to expose themselves to winter temperatures because of the behavior patterns previously discussed. They must survive the hardest and coldest parts of the winter and early spring eating on the cones of giant sequoias, as they do not store other conifer cones and have most likely used up any stored fungi by that time. A 250 g male could get 120 kcal/day eating the outer portions of 5 to 8 cones, if eaten under ideal conditions. The number of cones required depends on their size, the temperature, where they were consumed, and the insulation of the animal's nest. Just manipulating the cone while eating it is moderately hard work for the squirrel and requires a considerable output of energy.

Eating such a food source in cold temperatures may greatly reduce the net gain of energy involved in the process. Such a constant but just adequate food supply results in an inverse relationship between survival and the severity of winter weather. Cold winters, late snow packs and late springs were correlated somewhat strongly with decreases in numbers.

No estimate can be given for the level of predation by mammalian predators during the winters. Pine martins (*Martes americana*) are considered by Ingles (1965) to be predators on Douglas squirrels and may have contributed to mortality, especially in the winter of 1966-67.

There must be other factors in addition to those already discussed. These animals, for example, may undergo cyclic fluctuations, although the time frame of the study was too short to show if this was the case. It is difficult to explain the drop in numbers to near zero in 1974 from the very low population in 1973 on the basis of weather alone. The winter of 1973-74 was the most typical one of the ten-year period, and much milder than the harsher winters that preceded other declines. The decrease in cone cutting behavior, however, that was associated with low densities may have made the animals more prone to winter death.

In summary, the Douglas squirrels living in groves of giant sequoias differ considerably from their counterparts in other types of forests. They do not build large tree nests nor store the cones of conifers other than those of the giant sequoia. Cones are cut in greater numbers in years of high densities of squirrels, and the cones become almost more of a territorial object than a food source. The animals eat the fleshy outer parts of the green cones and some, but not significant amounts, of the tiny seeds. They may cut as many as 10,000 cones or more in a five-year period from a single tree, but their overall effect is slight in that they cut but 200 cones on the average per tree per year. This number is far less than the estimated 1,500 new cones added to the average tree each year. Many to most of the seeds in the cones are released relatively unharmed as the cones are eaten, and may contribute in a minor way to regeneration during brief periods of the year. The numbers of Douglas squirrels living in a grove fluctuate, apparently in response to weather and other unexplained factors. Giant sequoia cones appear to constitute a near minimal diet in most winters. Squirrel numbers do not seem to be affected by the use of fire and associated manipulations to the extent used in this study.

# Conclusions and Management Implications

*H. Thomas Harvey*

## *Conclusions*

### Introduction

The conclusions presented here are based on the findings from this and other studies. They include specific new facts about the giant sequoia and associated organisms, as well as inferences as to the relationship of physical and biotic factors to the perpetuation of this unique species. Both facts and inferences are offered as bases for interpretation of the life of the giant sequoias and for their management. One of the prime concerns is that of the position of giant sequoia in the successional pattern of western coniferous forests.

### Successional role of giant sequoias

Our studies support the widely held belief that the giant sequoia (*Sequoiadendron giganteum*) is a fire subclimax species of the middle elevation mixed coniferous forests of the central and southern Sierra Nevada (Hartesveldt 1964; Kilgore 1970, 1973). The particularly high seedling survival rate in burn pile soils—about 10 times that of seedlings on other manipulated substrates—along with the almost total absence of seedlings from the undisturbed forest floor, show the dependence of the giant sequoia on periodic fire for successful reproduction. Burn pile soils probably approach natural conditions where heavy fuel loads have accumulated. Although giant sequoia seeds may fall throughout the year at a rate approaching 1,000,000 seeds per hectare, their germination and subsequent seedling survival are minimal without the aid of fire. Thus fire, and apparently the hotter the better, is the prime requisite for the reproduction of sufficient seedlings so that the species may survive.

Older sequoia trees may persist long enough so that they remain as relicts in climax stands of white fir (Hartesveldt 1962; Bonnicksen 1975). Their contribution to the perpetuation of the species is probably minimal unless some major disturbance occurs to the forest floor. If this does not occur for prolonged periods of time, thick reproduction of white fir and other shade tolerant species can become established, and heavy concentrations of fuel may accumulate. As a shade intolerant species, but rel-

atively more resistant to fire than other trees, the giant sequoia is favored by such factors as fire which set succession back to an earlier stage.

### Role of animals in giant sequoia reproduction

The animal species which appear to affect the giant sequoia in either the seed or the seedling stage are relatively few in number. The early instars of the true bug *Ischnorrhynchus resedae* feed upon the endosperm of seeds in open cones in the tree. The small long-horned beetle (*Phymatodes nitidus*) and the Douglas squirrel (*Tamiasciurus douglasii*) mainly feed on the cones but not the seeds. In so doing they provide a continuous seed dispersal force. A squirrel may feed on an average of 200 cones per large tree per year, thus releasing about 40,000 seeds per tree. On the other hand, beetle activity may release about 120,000 seeds per tree per year. Neither species damage or consume a significant proportion of the seeds. In spite of this continual supply of seeds to the forest floor, very few are likely to survive unless some disturbance exposes mineral soil. During dry years very few seedlings appear in the undisturbed ground surface, however with exceptionally high precipitation as many as a thousand seedlings per hectare may spring up. Due to desiccation and insect and fungal attacks very few if any seedlings are apt to survive more than a year or so.

In addition to releasing seeds, some animal activity reduces a tree's production of seeds. For example, the gelechiid moth (*Gelechia* sp.) attacks first-year cones which results in the release of seeds that are non-germinable. Some moth infestation causes extended browning of cones and release of germinable seeds. This is a minor contribution to seed release.

Two species of moth caterpillars (*Sabulodes caberata* and *Pero behresarius*) and a camel cricket (*Pristocauthophilus pacificus*) were found active during the seedling stage. In a wet year the mortality of seedlings due to such insect activity was about 25%. This was second only to desiccation as a mortality factor. It is hypothesized that only in the first few years after fire, when giant sequoia seedlings are disproportionately plentiful while other plants are in short supply, the sequoias are heavily used as insect food. After two or three years have passed, sequoia seedlings are greatly reduced in number and other plant species have increased to the point that they then serve as the major insect food.

### Survival strategies of the giant sequoia

The giant sequoia has apparently evolved a set of adaptations which enable it to survive and prosper after fire sweeps through the forest. It has developed a cone which reduces seed loss while insuring seed release when eaten by animals. These two strategies involve an explosive reproduction and a repeated reproduction, respectively. The explosive repro-

duction follows fire, when numerous cones are opened by the heat of the fire and the ground is cleared of litter and duff so that the millions of seeds released will fall on an optimal substrate. The repeated reproduction strategy involves continual release of seeds by the action of animals and the fortuitous combination of optimal soil moisture and light, combined with disturbance of the forest floor. An example of this latter type of reproduction is found in the falling of a large sequoia at the edge of a meadow. Mineral soil is exposed to seeds with ample light and soil moisture to insure their germination and the subsequent survival of the seedlings.

The giant sequoia is similar to most organisms in having reached a compromise between K selection and r selection (Krebs 1972). It appears to be K selected in its population constancy, large body size, repeated reproduction, and great age. It appears to be r selected in its survivorship curve (type III, high early stage mortality), rapid development, high  $r_m$ , and relatively early reproduction.

Serotinous cones have been evolved in the giant sequoia, as was first suggested by Shellhammer. They differ from those evolved by other conifers in that they function not so much as deterrents to seed predation by rodents, but rather as a type of cone in which the scales have become a food source in themselves. The closed-cone pines have evolved cones which, because of being enlarged and hard, reduce the loss of seeds due to predation (Smith 1970; Daubenmire 1974). Giant sequoias, however, in providing a source of food in the cone scales, seem to be able to take advantage of the feeding activity of Douglas squirrels and beetles to assure a continuous release of seeds. This, along with the long period of time over which closed cones with germinable seeds may persist, coupled with large cone crops (up to 40,000 per tree per year) and numerous seeds per cone (200 on the average) make the giant sequoia fit not only for continuous reproduction but also provide it with a reservoir of large numbers of seeds for propagation when a fire releases them and sweeps the forest floor clean.

The apparent co-evolution of three animal species that feed on sequoia cones reduces competition for a food source and aids the sequoia in its repetitive reproduction strategy. Although early infestations of the gelechiid moth may bring about the release of nongerminable seeds, successful infestations may induce release of germinable seeds from second-year cones. The Douglas squirrel feeds mostly on cones that are from two to five years old, while the long-horned beetle feeds on cones four years and older. These three species apparently have partitioned the food source on a basis of age of cone, with each in turn taking a greater and greater percentage of the cone crop with increasing age of the cones. Therefore, as soon as seeds become germinable there is a continuous sequence of animals feeding upon the cones that releases a constant supply of such seeds upon the ground. This persistent fall of seeds provides reproduction

during the occurrence of favorable situations on the forest floor, and thus is a vital part of the repetitive reproduction strategy.

Hot fires beneath giant sequoias may heat closed cones to the extent that they die, dry out and release their seeds much in the fashion of the closed-cone pines (Daubenmire 1974). The additional adaptations of thick bark and evanescent branches enable mature trees to resist fire and serve as a continuing source of seeds for thousands of years. The tree produces cones which are serotinous and are therefore present many years after the seeds become germinable. The annual crop of cones is added to those that persist from previous years to provide an accumulation of tens of thousands of cones per tree. These numerous closed cones are then available to shed seeds if a hot fire comes through and dries them out. Our evidence that the hottest fire conditions produce the most favorable substrate for seedling survival, when coupled with serotinous cones, indicates that giant sequoias are adapted for explosive reproduction.

## *Sequoia management*

### Fire management policy

The concept of fire as a management tool in western forests was first developed by Weaver and Kallander during the 1940s (Kilgore 1976). Their principal objective was to reduce the hazards of wildfires. In California the leader in investigating prescribed fires was H.H. Biswell, whose work started in 1951 in ponderosa pine forests (Kilgore 1976). The study reported here, which started in 1964, was also aimed at reducing wildfire hazards, but in addition, emphasis was given to understanding the effect on giant sequoia reproduction. The role of fire in sequoia groves is now seen to include both fuel reduction and enhancement of giant sequoia regeneration. Thus the use of fire as a management tool in sequoia forests may serve the role of reducing wildfire hazards while at the same time producing for a relict species, the giant sequoia, the natural conditions under which it seems to have evolved and upon which it depends for its survival.

Inasmuch as the majority of giant sequoias are under the jurisdiction of the National Park Service, management policy will be mainly discussed in that context. The other two governmental agencies with management decisions over the species are the State of California and the United States Forest Service. The use of prescribed fires as a management tool in sequoia groves by these agencies began in 1975. In that year the Forest Service conducted a small test fire in the Nelder Grove near Yosemite National Park. Also in 1975 the California Department of Parks and Recreation, under H.H. Biswell's direction, used prescribed burns in the South Calaveras Grove.

The fire policy of the National Park Service has gradually shifted from fire exclusion to fire inclusion. Beginning in 1886 in Yellowstone the policy

was to suppress all fires (Agee 1974). The National Parks Act of 1916 emphasized the protection of objects, including trees, rather than processes. Therefore the early emphasis was on trying to perpetuate the status quo without fully appreciating the inexorable process of succession.

Kilgore (1976) reports that ". . . present National Park Service fire management policy divides all fires into management fires or wildfires. It defines management fires as those of both natural origin and prescribed burns which contribute to the attainment of the management objectives of a park through execution of predetermined prescriptions defined in detail in a portion of the approved resources management plan." This policy allows some natural fires to burn, recognizes prescribed burning as an appropriate management tool and continues wildfire suppression in developed areas. Wildfire suppression may also be necessary in undeveloped areas where fuel levels have built up to the point where natural, lightning-caused fires might become so intense as to destroy the entire forest community.

Natural fires above about 2600 m (8,000 ft) in Sequoia and Kings Canyon National Parks have been allowed to burn since 1968, while prescription burning has been employed at lower elevations (Kilgore and Briggs 1972). These policies have resulted, by 1975, in the prescription burning of about 5,400 ha (13,730 acres) outside the Natural Fire Management Zone of the two parks (Shuft 1973; Parsons pers. comm.).

According to Kilgore and Sando (1975), the use of prescribed burns can be instrumental in reducing the probability of crown fires and the high intensity of surface fires. However, in as little as 5–8 years enough litter may fall to the ground, in part induced by the prescribed burn, to bring the ground fuel level back to that preceding the fire (Kilgore 1975; Kilgore and Sando 1975). Therefore it follows that repeated prescribed fires may be needed to reduce this fuel load until a natural fire frequency may be attained (Kilgore 1975).

Several criteria should be met in order to implement an effective fire management program in giant sequoia groves. Basically an overall policy on fire must be developed by the agency with jurisdiction over each of the groves. Different agencies have different objectives and therefore will probably develop different policies which will be codified in their management program. In the National Parks the overall tone was set by the Leopold Report of 1963 (Kilgore 1976). The report called for re-creation of primitive America and noted the unnaturally dense growth of shade tolerant trees on the west side of the Sierra which has resulted from over-protection from natural surface fires. Valid objectives could include restoration of open forests, reduction of fire hazards, increased giant sequoia reproduction, and perpetuation of a given vegetation mosaic. Once the objectives of fire management and control are agreed upon, then an inventory map of the understory fuel types should be prepared (van Wag-

tendonk 1974). Blocks or strips to be burned must be carefully chosen to take into account topography, fuels and vegetation type. If a certain vegetation mosaic is an objective, then certain blocks may have to be left unburned.

If prescription burning is to be implemented, a detailed burning plan must be developed. This should include the objectives of the burn and the approximate dates during which the burning may be conducted. A prescription appropriate to the area should be developed and refined as burning is applied to the blocks within the area in question. At the actual time of burning, fuel stick moisture, relative humidity, wind velocity, and temperature must be assessed to be assured that they fall within the prescription parameters. If they do not, consideration should be given to immediate suppression activity.

In addition to the prescription fires, natural fires may be allowed to run their course provided they are within the Natural Fire Zone of a park and meet the objectives of the Management Program. Such fires should be closely monitored, and an appropriate committee should evaluate the impact of a given fire with the options to suppress, limit or allow continuation of the fire.

According to Henrickson (1972), the giant sequoia is a good example of the need for fire to preserve a species. He further adds that the fauna dependent on it, although of secondary importance, is almost neglected. Our studies indicate that the fauna is not greatly disturbed by small fires and that only a few of its species appear to be dependent on the earliest stages in succession, and they are not restricted to it. Therefore, the fauna associated with the giant sequoia, with the exception of a few insects, could probably survive even if the giant sequoia became extinct. Indeed, Bendell (1974) suggests that most vertebrate animals in coniferous forests are broadly adapted and persist through the changes induced by fire. The sequoia ecosystems have been subject to fires apparently for millions of years, and thus it is to be expected that organisms that are a part of that ecosystem have evolved to fit the alterations brought on by fire. One inference that can be drawn, however, from Bendell and our studies is that small patchy fires favor wildlife. This is in keeping with current guidelines proposed by Briggs (pers. comm.) that small strips not exceeding 30 m (100 ft) in width be employed, and that they be burned from the top down. This type of burning would allow wildlife to leave the fire area and then return, particularly if the fire has been somewhat patchy in its effect.

### Succession and management

The studies by Bonnicksen (1975) on the pattern of succession in a giant sequoia-mixed conifer forest indicate that it consists of a mosaic of even-aged stands of different species. Our studies indicated that, at the level

of treatment which was given, early-stage plants, e.g. annuals and shrubs, disappear or begin to be reduced within ten years. Giant sequoias, after developing in great numbers initially, are in less than 10 years reduced to only about 5% of the original seedling population. Kilgore (1973) reported even greater mortality, with 98% of the 54,000 seedlings dying within two years after a fire-induced population had been established. In our study the distribution of surviving trees is patchy, with thickets of sequoia saplings occupying burn pile soils and few surviving elsewhere. These relatively dense stands exemplify the mosaic pattern of reproduction identified by Bonnicksen (1975).

The general pattern of giant sequoia succession is that of patchiness. Rarely are substrate conditions uniform in a sequoia grove, even though it may have the same general climate. In addition, disturbance factors such as fire, disease and windfall generally occur in a patchy manner. The result of this nonuniform environment is a mosaic of vegetation types or successional stages. The implication of this pattern for management is that fire as a tool probably should not be applied evenly in a short period of time throughout a large area. Prescription fires should be applied in a patchy manner thus coming closest to re-establishing the primitive mixed conifer forest. The overall long term goal should be the establishment of conditions that would allow natural processes to operate uninterrupted in the ecosystem. The intensity and extent of treatment will be an important determinant in the response of the vegetation. Thus it is important to clearly identify the objectives of any given management burn before carrying it out.

### Hazard trees

The immense size of the branches of the giant sequoia may cause damage to property and injury or even death to people. Falling sequoias may do the same. The factors that may interact in causing trees and branches to fall are varied. Roots infected by fungi may weaken support, fire scars sever root connections, heavy snowfall overload crowns, winds blow down trees, streams undercut root systems, carpenter ants weaken wood by excavation of galleries, and wet soils provide minimal support. Recent studies by Piirto (pers. comm.) specifically implicate *Fomes annosus* in root failures in many giant sequoias.

In 1969 four giant sequoias, or portions of them, fell and resulted in the death of a woman. One tree, with a lean toward the fire scar side and carpenter ant and fungal activity at the plane of failure, fell and knocked the top section out of a neighboring tree which in turn struck and killed the woman. However prone to falling this tree may have been, there are numerous cases where leaning fire-scarred trees have not yet fallen. There are also cases where upright, apparently sound trees have fallen. It seems prudent to minimize the probability of injury and damage by removing

heavy, prolonged human activity from sequoia groves, particularly from areas of hazard tree concentrations.

## *Summary of findings*

### Natural history concepts

The giant sequoia is a relict species both geologically and successional. Only remnant populations of a once widespread species that spanned the northern hemisphere now persist on the western slope of the Sierra Nevada of California. In these remaining groves succession tends to lead toward replacement of the giant sequoia by shade tolerant species such as white fir. The ability to live for several thousand years and grow to be the tallest tree in the forest enables the giant sequoia to remain as a relict in the successional sense.

Two reproductive strategies seem apparent in the life cycle of this species. Repeated reproduction may occur as trees fall over and provide a suitable substrate and open up the canopy so that seedling sequoias may survive. Other disturbances to the forest floor also may enable seedlings to become established, e.g. deposition of sandbars in a river. The second strategy is operative when surface fires of fairly high intensity burn through sequoia groves. The serotinous cones provide an abundant source of seeds which may be released by the heat of the fire to provide for an explosive reproduction of the tree and for grove expansion.

Although in general the perimeters of giant sequoia groves appear to be relatively stable, the youngest trees exist on the edge in a few specific cases. Such trees were dated as being about 100 years old and their beginning coincided with the last fire in the areas in question. It therefore appears that expansion of groves is possible if conditions become favorable for seedling growth.

Seedfall apparently occurs throughout most of the year mainly due to the drying of cones after they have been attacked by the small long-horned beetle, *Phymatodes nitidus*. Contrary to Boe (1974), seeds are not released by drying of cone scales in the fall of the year. He misquotes Buchholz (1938). Buchholz was only speculating that such a thing might happen, but then went on to say that old cones, even over 20 years old, have near normal numbers of seeds in them. Our studies indicate that squirrel activity augments that of the beetle to provide the constant seedfall.

Seeds which have fallen to the ground may be exposed to sunlight and desiccation prior to germination. These factors, plus the apparent low germination percentage of seeds released from the cone, result in low viability of seeds at the ground level. This may be due in part to the mode of action of releasing seeds from the trees. The action of the beetle causes the cones to dry and cone scales to shrink. The seeds are then exposed

to the air and may lose their viability while still in the tree. Seed tests at the ground showed only about 1% viability. Given 1,000,000 seeds, however, this potential would yield 10,000 seedlings per hectare per year if conditions were favorable for their establishment.

The factors which either inhibit seed germination or seedling establishment in unburned areas can only be alluded to at this time. Desiccation appears to terminate most of the seedlings in the burned areas and probably is equally effective in unburned sections. It may be even more effective, for as Stark (1968b) has shown, giant sequoia seeds will germinate in the duff and litter if adequate moisture is present. The developing seedlings however, would be more subject to desiccation inasmuch as more of the root would not be in contact with the mineral soil.

Insect feeding on, and sun scald of seedlings would probably be less in an unburned area than in a recently burned site. Stark (1968a) reported less sun scald in seedlings when litter was present. Insect feeding and sun scald were mortality factors in burned sites, although at a much lower level of intensity than desiccation.

Both light conditions and allelopathic substances hypothetically should be more adverse to seedlings in unburned areas than in burned. Lower light intensity could induce shorter roots and thus greater chance of desiccation. Allelopathic substances might also build up in unburned soils.

The one factor which appears to release the greatest number of viable seeds quickly and to prepare the best of seedbeds for the giant sequoia is fire. And given the fire adaptations of the tree—thick fire resistant bark and high canopy—seldom is much severe damage done to the mature trees.

Prescription burns of relatively small size (10 ha) apparently have little effect on bird and mammal populations, which agrees with conclusions made in other similar studies (Kilgore 1971; Bendell 1974; Vogl 1973). The mosaic of fire intensities caused by the existing vegetation mosaic allow animals to flee to refugia during fires. The extensive use of fire probably would increase the numbers of woodpeckers, flycatchers and other insectivorous birds and ground squirrels. The greater the intensity of the fire, the earlier the stage in the successional pattern that will be developed.

The Douglas squirrel is the only vertebrate that appears to exert much of an effect on sequoia reproduction. The small size of the seeds and their wide dispersal and their loss in the litter and duff make them of minimal food value to mammals. Rodents show a very low interest in sequoia seeds, apparently preferring the larger seeds of the other conifers in the mixed conifer forest of the mid-elevations of the Sierra Nevada.

Few giant sequoia seedlings were observed to be eaten by vertebrates. Vertebrate predation accounted for less than 2% of the mortality of one

to three year old seedlings. Only immediately after a fire, when other ground food sources were reduced and giant sequoia seedlings were abundant, did vertebrates ever seem to turn to them for food.

Douglas squirrels store only giant sequoia cones in a sequoia-mixed conifer forest. Although they were observed eating the seeds of other conifers, no caches were found other than of giant sequoia cones. They feed on sequoia cones throughout the year, leaving them only as other food sources come to maturity. Other foods included fungi and seeds or fruits of such nonconifers in season as hazelnuts. The preoccupation of sequoian squirrels with giant sequoia cones marks them as rather distinct behaviorally, probably as the result of early learning on the part of young squirrels. Their feeding on sequoia cones probably has a minimal effect on the giant sequoia as only about 200 cones per tree per year are eaten. However, as high as 2,000 cones may be cut from one tree during a year. No nests of the Douglas squirrel were observed other than in a cavity in a large sequoia.

Territoriality was strongly exhibited by Douglas squirrels in high population years. The giant sequoia appeared to be the stimulus and focal point of their agonistic behavior. Only one squirrel ever occupied a given large giant sequoia, loudly fending off any would-be intruders. When populations were small, possibly due to severe winters, and squirrels were widespread, their territorial behavior dropped practically to zero, and they moved between several giant sequoias and reduced their caching activities.

The insect fauna associated with the giant sequoia is highly variable. As discussed earlier a few insects affect seed production and early seedling growth. Once the tree is grown, a relatively small but fascinating fauna develops. Several fluid-feeding insects concentrate on the lower foliage of mature trees. Aphids, treehoppers and true bugs had representatives in this category, while chewing insects such as geometrids and leaf beetles were concentrated in the upper portion of the crown.

In conclusion, our findings indicate that cone predation by animals is somewhat partitioned among them so that competition is minimized between predators. First year cones are utilized by a moth, while cones 2 to 5 years old are fed upon by Douglas squirrels, and older cones (4 to 11 yrs) are the domain of a minute long-horned beetle. The squirrel exploits the cones primarily for the food value of the cone scales, thus releasing the seeds. The beetle mines throughout the cone and in so doing interrupts the vascular system which may sustain the cone in a green, closed condition for over 20 years. When the vascular system is severed the cone turns brown and the scales shrivel and release their seeds. Therefore, through the activity of the beetle and the squirrel there is a constant release of seeds. The establishment of seedlings, however, is best after a fire, which also may release seeds. Without fires intense enough to open the canopy, shade killing of young sequoias may occur and leave only

sequoias as successional relicts surrounded by shade tolerant white firs. For these reasons it is essential that fire be re-introduced in its natural role if the sequoia ecosystem is to survive in anything resembling its primitive state.

## Appendix I

**Alphabetical Listing of Flowering Plants\***  
**Giant Sequoia Regeneration Plots**  
**Kings Canyon National Park**

Scientific Name	Common Name	Family
<i>Abies concolor</i>	White fir	Pinaceae
<i>Adenocaulon bicolor</i>	Trail plant	Compositae
<i>Agoseris retrorea</i>	Mountain dandelion	Compositae
<i>Alliophyllum integrifolium</i>		Polemoniaceae
<i>Amelanchier pallida</i>	Service-berry	Rosaceae
<i>Apocynum androsaemifolium</i>	Dogbane	Apocynaceae
<i>Aquilegia formosa</i>	Columbine	Ranunculaceae
<i>Arabis repanda</i>	Rock-cress	Cruciferae
<i>Arctostaphylos patula</i>	Greenleaf manzanita	Ericaceae
<i>Asarum hartwegii</i>	Wild ginger	Aristolochiaceae
<i>Bromus laevipes</i>	Brome grass	Gramineae
<i>Calocedrus decurrens</i>	Incense cedar	Cupressaceae
<i>Carex bolanderi</i>		Cyperaceae
<i>Castanopsis sempervirens</i>	Sierra chinquapin	Fagaceae
<i>Castilleja disticha</i>	Paint brush	Scrophulariaceae
<i>Ceanothus cordulatus</i>	Mountain white thorn	Rhamnaceae
	Snow bush	
<i>Ceanothus integerrimus</i>	Deer brush	Rhamnaceae
<i>Ceanothus parvifolius</i>	Sweet birch	Rhamnaceae
	Small-leaved ceanothus	
<i>Chamaebatia foliolosa</i>	Mountain misery	Rosaceae
	Bear mat	
<i>Circaeа alpina</i> var. <i>pacifica</i>	Enchanter's nightshade	Onagraceae
<i>Cirsium vulgare</i>	Bull thistle	Compositae
<i>Clintonia uniflora</i>	Bride's bonnet	Liliaceae
<i>Collinsia childii</i>		Scrophulariaceae
<i>Collinsia torreyi</i>		Scrophulariaceae
<i>Convolvulus malacophyllum</i>	Sierra morning glory	Convolvulaceae
<i>Corallorrhiza maculata</i>	Spotted coral root	Orchidaceae
<i>Cornus nuttallii</i>	Mountain dogwood	Cornaceae
<i>Corylus cornuta</i>	Hazelnut	Betulaceae
<i>Cryptantha affinis</i>		Boraginaceae
<i>Disporum hookeri</i>	Fairy bells	Liliaceae
<i>Draperia systyla</i>		Hydrophyllaceae
<i>Equisetum hyemale</i>	Horsetail	Equisetaceae
<i>Eriogonum latifolium</i>	Wild buckwheat	Polygonaceae
<i>Erysimum perene</i>	Western wall flower	Cruciferae
<i>Festuca occidentalis</i>	Fescue	Gramineae
<i>Galium sparsiflorum</i>		Rubiaceae

\*Scientific names after Munz (1959).

Scientific Name	Common Name	Family
<i>Galium triflorum</i>	Sweet-scented bedstraw	Rubiaceae
<i>Gayophytum nuttallii</i>		Onagraceae
<i>Goodyera oblongifolia</i>	Rattlesnake-plantain	Orchidaceae
<i>Habenaria unalascensis</i>	Rein orchis	Orchidaceae
<i>Hackelia mundula</i>	Stickseed	Boraginaceae
<i>Hieracium albiflorum</i>	Hawkweed	Compositae
<i>Hydrophyllum occidentale</i>	Waterleaf	Hydrophyllaceae
<i>Juncus effusus</i>	Rush	Juncaceae
<i>Linanthus montanus</i>	Yellow-throated gilia, Mustang clover	Polemoniaceae
<i>Lotus purshianus</i>	Bird's foot trefoil	Leguminosae
<i>Lupinus latifolius</i> var. <i>columbianus</i>	Lupine	Leguminosae
<i>Mimulus bicolor</i>		Scrophulariaceae
<i>Mimulus moschatus</i>	Musk flower	Scrophulariaceae
<i>Mitella breweri</i>	Mitewort	Saxifragaceae
<i>Montia gypsophiloidea</i>		Portulacaceae
<i>Montia perfoliata</i>	Miner's-lettuce	Portulacaceae
<i>Montia spathulata</i> var. <i>tenuifolia</i>		Portulacaceae
<i>Osmorrhiza chilensis</i>	Sweet-cicely	Umbelliferae
<i>Phacelia mutabilis</i>		Hydrophyllaceae
<i>Pinus lambertiana</i>	Sugar pine	Pinaceae
<i>Pinus ponderosa</i>	Ponderosa pine	Pinaceae
<i>Pleurocospora fimbriolata</i>	Five-finger, Cinqfoil	Pyrolaceae
<i>Potentilla glandulosa</i>	Fern	Rosaceae
<i>Pteridium aquilinum</i> var. <i>lanuginosum</i>		Pteridaceae
<i>Pterospora andromedea</i>	Pinedrops	Pyrolaceae
<i>Pyrola picta</i>	White-veined shin-leaf	Pyrolaceae
<i>Quercus chrysolepis</i>	Canyon live oak	Fagaceae
<i>Quercus kelloggii</i>	California black oak	Fagaceae
<i>Ribes roezlii</i>	Sierra gooseberry	Saxifragaceae
<i>Rosa californica</i>	Rose	Rosaceae
<i>Rosa pinetorum</i>	Wild rose	Rosaceae
<i>Rubus glaucifolius</i>	Raspberry	Rosaceae
<i>Rubus leucodermis</i>	Western raspberry	Rosaceae
<i>Rubus parviflorus</i>	Thimbleberry	Rosaceae
<i>Sambucus caerulea</i>	Elderberry	Caprifoliaceae
<i>Sequoiadendron giganteum</i>	Giant sequoia	Taxodiaceae
<i>Silene bridgesii</i>	Catchfly	Caryophyllaceae
<i>Silene lemmonii</i>	Catchfly	Caryophyllaceae
<i>Smilacina racemosa</i> var. <i>amplexicaulis</i>	False Solomon's seal	Liliaceae
<i>Stachys albens</i>	Hedge nettle	Labiatae
<i>Stellaria jamesiana</i>	Chickweed	Caryophyllaceae
<i>Symporicarpos acutus</i>	Snowberry	Caprifoliaceae
<i>Viola lobata</i>		Violaceae
<i>Viola purpurea</i>	Violet	Violaceae
<i>Viola sheltoni</i>	Shelton's violet	Violaceae

## Appendix II

## Insects Associated with Giant Sequoias

Order Family Species	Name	Location	Remarks
		Downed Trees	
		Seedlings	
		Trees under 25 ft	
		Trees 25-100 ft	
		Trees 100-300 ft	
Collembola			
Entomobryidae	<i>Entomobria</i> sp.		X X on bark, entire tree
Orthoptera			
Gryllidae	<i>Myrmecophila oregonensis</i> Bruner	X	under loose bark with ants
Gryllacrididae	<i>Pristocaulophilus pacificus</i> Thomas	X	early instars eat seedlings
Isoptera			
Kalotermitidae	<i>Zootermopsis navadensis</i> (Hagen)	X	drywood termites
Hemiptera			
Berytidae	<i>Neides muticus</i> Say	X X X	stiltbug, small predator
Nabidae	<i>Nabis ferus</i> (Linnaeus)	X X X	small predator
Miridae	<i>Lygeus hesperus</i> Knight	X X X	feeding on new foliage
Lygaeidae	<i>Ischnorrhynchus resedae</i> (Panz)	X X X	in open cones and foliage
Pentatomidae	<i>Thyanta pallidovirens</i> (Stål)	X X X	in foliage

Order Family Species	Name	Location	Remarks		
			Downed Trees	Seedlings	Trees under 25 ft
<b>Homoptera</b>					
<b>Cicadellidae</b>					
	<i>Aceratagallia longula</i> Van Duzee		X	X	feed on foliage fluid
	<i>Aceratagallia</i> spp.			X	feed on foliage fluid
	<i>Empoasca</i> sp.	X	X	X	feed on foliage fluid
	<i>Brenda arborea</i> (Ball)			X	feed on foliage fluid
	<i>Colladonus flavocapitatus</i> (Van Duzee)			X	feed on foliage fluid
	<i>Colladonus</i> sp.	X	X		feed on foliage fluid
	<i>Idiocerus musteus</i> Ball	X	X	X	feed on foliage fluid
	<i>I. apache</i> Bell & Parker			X	feed on foliage fluid
	<i>I. amoenus</i> Van Duzee	X	X	X	feed on foliage fluid
	<i>I. nervatus</i> Van Duzee	X	X		feed on foliage fluid
	<i>Balclutha medius</i> Baker	X	X	X	feed on foliage fluid
	<i>Pagaronia confusa</i> Oman	X			feed on foliage fluid
	<i>Paraphlepsius apertinus</i> Osborn & Lathrop	X			feed on foliage fluid
<b>Cercopidae</b>					
	<i>Aphrophora maculosa</i> Doering	X			feed on foliage fluid
	<i>Clastoptera siskiyou</i> Doering	X	X		feed on foliage fluid
<b>Achilidae</b>					
	<i>Epiptera fusiformis</i> (Van Duzee)			X	feed on foliage fluid
<b>Issidae</b>					
	<i>Dyctidea</i> sp.		X		feed on foliage fluid
<b>Membracidae</b>					
	<i>Platycotis minax</i> Goding	X			feed on foliage fluid
	<i>Micruitalis occidentalis</i> Goding	X			feed on foliage fluid
	<i>Crystolobus nitidus</i> Van Dyke				feed on foliage fluid
<b>Psyllidae</b>					
	<i>Psylla brevistigmata</i> Patch			X	feed on foliage fluid
<b>Aphididae</b>					
	<i>Masonaphis morrisoni</i> Swain	X	X	X	X most common insect in tree. Feed on foliage fluid.

	Name	Location	Remarks	
Order		Downed Trees	Seedlings	Trees under 25 ft
Family				Trees 25-100 ft
Species				Trees 100-300 ft
	<b>Coccidae</b>			
	<i>Aonidia shastae</i> (Coleman)	X	X	by DeLeon 1952
	<i>Diaspis carueli</i> Targ.	X		by DeLeon 1952
	<i>Aonidiella aurantii</i> (Maskell)	X		by DeLeon 1952
	<i>Cryptaspidotus shastae</i> (Coleman)	X		by DeLeon 1952
	<i>Hemiberlesia rapax</i> (Comstock)	X		by Coleman 1903
	<i>Carulaspis visci</i> (Schrank)	X		by DeLeon 1952
	<b>Neuroptera</b>			
	<b>Raphidiidae</b>			
	<i>Agulla assimilis</i> Banks	X	X	X predators
	<b>Chrysopidae</b>			
	<i>Chrysopa carnea</i> Stephens	X	X	X predators
	<b>Hemerobiidae</b>			
	<i>Hemerobius pacificus</i> Banks	X	X	X predators
	<b>Lepidoptera</b>			
	<b>Geometridae</b>			
	<i>Semiothisa muscariata</i> Gn.		X	X defoliator
	<i>Sabulodes caberata</i> Gn.	X		feed on seedlings
	<i>Pero behresarius</i> Packard	X		feed on seedlings
	<i>Nemoria</i> sp.	X	X	X defoliator
	<b>Noctuidae</b>			
	"Cutworms"	X		damage to nursery stock by Fry & White 1931
	<b>Arctiidae</b>			
	<i>Halysidota argentata</i> Packard	X		feeding in larval stage by DeLeon 1952
	<b>Yponomeutidae</b>			
	<i>Argyresthia</i> sp.			foliage feeder, DeLeon 1952
	<b>Gelechiidae</b>			
	<i>Gelechia</i> sp.	X	X	1st year cones only

Name	Location	Remarks
Order Family Species		
Coleoptera		
Rhysodidae		
<i>Rhysodes hamatus</i> Le Conte	X	under bark
Carabidae		
<i>Bembidion</i> sp.	X	under bark
<i>Pterostichus</i> sp.	X	X searching hole at night to 20 ft.
Coccinellidae		
<i>Olla abdominalis</i> (Say)	X	X feeding on aphids
Cantharidae		
<i>Cantharus</i> sp.	X	X X
Cleridae		
<i>Enoclerus shaefferi</i> Barr	X	X predators
<i>E. lecontei</i> (Wolc.)	X	X predators
<i>Cymatodera</i> near <i>sobara</i> Barr	X	X predators
Anthicidae		
<i>Anthicus</i> sp.	X	X
Dermestidae		
<i>Attagenus nigripes</i> Casey	X	
Ptinidae		
<i>Ptinus agnatus</i> Fall	X	X reared from small limbs
Rhizophagidae		
<i>Rhizophagus sculpturatus</i> Mannerheim	X	scavengers under moist bark
<i>R. near dimidiatus</i> Mannerheim	X	scavengers under moist bark
Tenebrionidae		
<i>Nyctoporis carinata</i> Le Conte	X	under bark
<i>Uloma longula</i> Le Conte	X	scavenger under bark
<i>Eleodes</i> sp.	X	scavenger under bark
Staphalinidae		
<i>Trigonurus</i> sp.	X	predator under bark

Order Family Species	Name	Location	Remarks
		Downed Trees Seedlings Trees under 25 ft	
		Trees 25-100 ft	
		Trees 100-300 ft	
Lampyridae	<i>Lycidota californica</i> (Mots.)	X	predator under bark
Cucujidae	<i>Cucujus clavipes</i> Mannerheim	X	predator under bark
	<i>Dendrophagus cygnaei</i> Mannerheim	X	predator under bark
Ostomatidae			
	<i>Temnochila virescens</i> (Fabricius)	X	predators under bark
	<i>Nemozoma fissiceps</i> (Fall)	X	predators under bark
Colydiidae	<i>Lasconotus vegrandis</i> Horn		X
Melasidae			
	<i>Melasis rufipennis</i> Horn	X	larvae bore heartwood
	<i>Dromaelus</i> sp.		X larvae in thick bark standing tree, DeLeon 1952
Elateridae			
	<i>Megapenthes quadrimaculatus</i> (Horn)	X	under bark
	<i>Ctenicera</i> sp.	X	under bark
Buprestidae			
	<i>Anthaxia aneogaster</i> (Lap-Gorg)	X X	
Lucanidae			
	<i>Ceruchus punctatus</i> LeConte	X	larvae bore heartwood
Scarabaeidae			
	<i>Dichelonyx vicinia</i> (?) Fall	X	new foliage
Chrysomelidae			
	<i>Glyptoscelis juniperi xanthocoma</i>	X	foliage feeder
	<i>Thricolema anomala</i> Crotch	X	feeding on new foliage
Cerambycidae			
	<i>Anoplodera valida</i> (LeConte)	X	larvae mine heartwood
	<i>Semanotus ligneus amplus</i> Casey	X	larvae in fresh down limbs

Order	Family	Species	Name	Location	Remarks
				Downed Trees Seedlings	Trees under 25 ft Trees 25-100 ft Trees 100-300 ft
			<i>Callidium sequoiarum</i> Fisher	X	larvae in fresh down limbs
			<i>Phymatodes nitidus</i> LeConte	X	X larvae mine cones
	Bostrichidae				
			<i>Scobicia declivis</i> (LeConte)	X	X on foliage & mines deadwood
	Scolytidae				
			<i>Phloeosinus punctatus</i> LeConte	X	X X mine dead limbs on ground and standing
			<i>Gnathotrichus sulcatus</i> (LeConte)	X	mine limbs to 2 ft. dia.
	Cucujidae				
			<i>Cionistes insolens</i> Dietz		X feeding on foliage
			<i>Thricolepis inornata</i> Horn	X X	feeding on foliage
			<i>Sitona californica</i> Fabricius	X	
			<i>Apion</i> sp.	X	
	Hymenoptera				
	Siricidae				
			<i>Sirex areolatus</i> (Cresson)	X	larvae mine into heartwood
	Formicidae				
			<i>Camponotus minor</i>	X	X breed chambers in old wood
			<i>Formica neorufibarbis gilida</i> Wheeler	X X	active on foliage & bole
			<i>Formica</i> sp.	X	X active on foliage & bole
	Xylocopidae				
			<i>Xylocopa californica</i> (Cresson)	X	X brood chambers in deadwood
			<i>X. orpifex</i> Smith		X dead top 12 ft dbh green tree (DeLeon 1952)
	Diptera				
	Bombyliidae				
			<i>Villa alternata</i> Say		X larvae about crown, larvae parasitic
	Acroceridae				
			<i>Acrocera</i> sp.	X	

Order	Name	Location	Remarks
Family			
Species			
		Downed Trees	
		Seedlings	
		Trees under 25 ft	
		Trees 25-100 ft	
		Trees 100-300 ft	
Lauxaniidae			
	<i>Minettia flaveola</i> (Coquillett)	X X X	very common throughout tree
Stratiomyidae			
	<i>Hermetia</i> sp.	X	under wet bark
Syrphidae			
	<i>Syrphus</i> sp.	X X	larvae eat aphids, adults active crown
Asilidae			
	<i>Neoitamus affinis</i> (Willieton)	X X	feed on <i>Syrphus</i> . adults in crown
	<i>Dioctria vera</i> Black	X X X	ambush site
	<i>Asilus</i> sp.	X	ambush site

(Note: About 35 additional forms await identification by specialists.)

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